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No. 28.

THE ANATOMY OF THE TORTOISE.

By J. STUART THOMSON, M.Sc., Ph.D., F.R.S.E.,
Formerly Senior Lecturer in Zoology in the Victoria University of Manchester.

(Plates 19–43.)

[Read May 24. Published December 30, 1932.]

Contents.

Introduction.

Section 1.—*External Characters.*

Systematic Position of the Genus Testudo—Distinctive characters of the species *Testudo graeca* and *ibera*—External characters—Shields of the Carapace—Shields of the Plastron—Regeneration of the Shields and Plates—Epidermic hard parts—The Salient Structural Features of the Chelonia.

Section 2.—*The Carapace and Plastron.*

Bony plates of the Carapace and Plastron — Homologies of the bony plates of the Plastron—Divergent views regarding the development and evolution of the Neural and Costal Plates of the Carapace of Chelonia.

Section 3.—*The Skull.*

The Skull from the posterior, dorsal, lateral, and ventral aspects—Foramina of the Skull—General characteristics of the Skull.

Section 4.—*The Vertebral Column.*

Cervical Vertebrae—Dorsal Vertebrae—Sacral Vertebrae—Caudal Vertebrae.

Section 5.—*The Limbs and Limb Girdles.*

The Pectoral Girdle of Testudo—Pectoral Girdle of Chelonia—general—Pelvic Girdle of Testudo—The Fore Limb—The Anterior Limb of Chelonia in general—The Posterior Limb.

Section 6.—*The Viscera and Alimentary System.*

The Viscera in situ—The Alimentary Canal—The Mesenteries—The Visceral arteries and veins—The Coelom—Pleuroperitoneal cavity—The Retroperitoneal condition.

Section 7.—*The Vascular System.*

The Venous System—The Arterial System—The Structure of the Chelonian Heart—The Lymphatic System—The Ductless Glands.

Section 8.—*The Buccal Cavity and Respiratory Organs.*

The Tongue—Lingual Muscles—Apertures in the Buccal Cavity—Glottis and other respiratory parts.

Section 9.—*The Reno-reproductive System.*

Female urinogenital organs—Ovaries—Oviducts—Kidneys—Adrenal Bodies—Ureters—Urinogenital Sinus—Urinary Bladder—Cloaca—Clitoris—Male genital organs—Testes—Epididymes—Vasa efferentia—Vasa deferentia—Urinogenital Sinus—Pelvis—The Cloaca and adjoining parts in Chelonia in general.

Section 10.—*The Nervous System—The Muscular System.*

The Spinal Cord—The Brain—The Origin of the Cranial Nerves—The Distribution of the Cranial Nerves—The Sympathetic Nervous System—The Cervical Nerves—The Brachial Plexus—The Dorso-lumbar Nerves—The Lumbosacral Plexus—Reference to the Muscular System.

Section 11.—*The Sensory Organs.*

Olfactory Organs—Stato-auditory Organs—The Eyes—Accessory Glands.

Section 12.—*Development.*

Development of the Turtle—Main Features in the Development of Chelonia.

Appendix.

Dissection of the Tortoise—Practical Suggestions.

Explanation of Plates.

References to Literature.

Introduction.

One may write a foreword to this study of the "Anatomy of the Tortoise" by referring to its every-day life. The Tortoise is a representative of an ancient order, dating from the early Mesozoic Period, and is one of the most inactive of all existing vertebrata, for it sleeps during two-thirds of its rather vegetative existence, and during the remaining third appears only half-awake—it seems like a reptilian prototype of "the fat boy" of the *Pickwick Papers*.

One of the many heavily armed creatures of the past, its type has persisted in spite of obvious ineptitude when compared with others of greater activity, with freer limbs and weapons of offence. Encased in their coats of horn and bone, from which they never can escape, Chelonia are survivals, whose race has to some extent been supplanted by creatures neither so slow in living nor in dying.

When the organs of the Chelonia are considered from the point of view of function, the following features are indicated:—The skin is equipped neither with temperature transmitters to regulate the internal production of heat, nor with temperature regulators to increase or decrease the escape of heat, consequently the temperature of the body and blood is not constant. Muscular activity is reduced and intermittent, and fewer muscles are called into action.

Locomotion is slow and cautious, and the forelimbs are slightly displaced from the normal position in the Vertebrata, owing to their cramped position within the "shell." As regards the brain and nervous system, the cerebral cortex is not peripheral, as in the Mammalia, and the Chelonia can scarcely be credited with intelligence; there also appears to be a certain lack of nervous or bodily integration, for tortoises can live and walk for months after removal of the brain, and the heart continues to beat after the animals have been decapitated. The capacity of regenerating injured parts of the "shell" is also noteworthy, The circulation of the blood is relatively slow, the arterial is not completely separated from the venous blood in the incompletely divided ventricle, and the arteries of the stomach and intestines receive only mixed blood. Respiration is handicapped by the rigidity of the carapace and plastron, which renders free movements of the thoracic and abdominal walls impossible; inspiration and expiration are effected through the protraction and retraction of the head and limbs, and when these movements are not taking place the animals carry on for long intervals without taking breath. The lungs are extensive, practically covering the entire dorsal surface, and one would suppose that there is a large residuum of air left in them, even after expiration has taken place. Cutaneous excretion is reduced in the absence of sudorific glands, but it is possible that the carapace and plastron in themselves may be partly regarded as formed from waste products. The blood stream to the kidneys is increased by the particular development, from the median azygous veins of an anterior renal portal, which connects with the kidneys at the anterior ends. A quantity of water is taken in at long intervals, and is stored for lengthy periods in the extremely large bladder. It is suggested that this is a store for dormant periods. The response to sensory impressions does not appear to be very keen, but the Chelonia show a greater awareness than might at first be suggested. There is evidence of the recognition of persons, places, and sounds. Most people have experience of the Chelonian's response to increase of temperature, and in this connection the disappearance of the Pond Tortoise, *Emys orbicularis,* from this country, and its persistence in Southern Europe, may not be surprising, for warmth at some period is a *sine qua non* of any Chelonian's existence. As regards reproduction and development, the pairing is prolonged, and the duration between fertilisation and the deposition of the eggs is lengthy, as also that between the latter and hatching. The Chelonia are secure against attack, save those of bacteria, ticks, birds, and human beings, but in ordinary circumstances their longevity goes without saying.

The structure of the Chelonians may be compared, system by system, with that of other Vertebrata without showing any very great divergence, save such as may be correlated with the differentiation of the "shell" (see text). As a general axiom, one may state that the rate of anabolism and katabolism is slow, and that the katabolic processes are slower than in almost any other vertebrate.

The chief prizes of life come not to those who live the "life of ease," passively taking shelter from the straits and strains, but to those with good

limbs and strong lungs who pursue their prey or run from danger or migrate; to those who fight with weapons, teeth, hoofs, horns, and claws, or with adaptable hands and brains.

The Greek and Iberian Tortoises are terrestrial, diurnal, vegetarian, winter-sleeping reptiles. They are hatched from the eggs, two to four months after these are laid, in the earth or leaves, and live some fifty or more years. Evidence of sensory impressions is seen in the recognition of persons, in distinction of food by scent, taste, and touch, in an awareness of, and sometimes apparent pleasure in, different sounds, in a response to sunshine or shade, drought or rain. They show a surprising memory for places, even at a distance, and a remarkable, and altogether mysterious, faculty of orientation. They show little or no parental care; their food consists by preference of succulent plants. They go to sleep before sunset, and awake long after dawn. The cold of approaching winter calls them to sleep, and the warmth of early summer to some measure of intermittent activity. When kept in captivity, they should be given winter quarters in decaying leaves or amongst hay.

Some have hazarded the suggestion that tortoises resemble military tanks; but surely any such similitude cannot be carried beyond, if as far as, the surface. It is scarcely surprising that such weird creatures should have intrigued the attention of the early naturalists.

Section 1.—External Characters.

Systematic Position of the Genus Testudo—Distinctive characters of the species *Testudo graeca* and *ibera*—External characters—Shields of the Carapace—Shields of the Plastron—Regeneration of the Shields and Plates—Epidermal hard parts—The Salient Structural Features of the Chelonia.

The Iberian and Greek Tortoises, *Testudo ibera* and *Testudo graeca*, described in this monograph, are the common species occurring in the English markets. Their Zoological position is as follows:—

Class	... Reptilia.	Family	... Testudinidae.
Order	... Chelonia.	Genus	... Testudo.
Sub-order	... Thecophora.	Species	... *ibera and graeca.*
Section	... Cryptodira.		

Testudo graeca.

The specific characters of the common "Greek Tortoise," *Testudo graeca*, are as follows:—Carapace very convex, shields without keels, and with smooth non-serrated margins. Anterior or nuchal shield narrow; the fifth or last neural shield much broader than the others. The last supracaudal shield usually divided in the mid-dorsal line, and is generally regarded as the last pair of marginals. Plastron notched behind, axillary and inguinal shields small.

Scales on anterior surface of the forelimbs small, arranged in six to ten longitudinal rows. Posterior surface of the thigh smooth, without a tubercle. Tip of tail ends in a horny conical spur. Coloration variable, plastron with an irregular, broad, black border. Centres of shields granular in young, smooth in older specimens; concentric lines of growth arranged around the centre (see Gadow). The so-called Greek Tortoise is not limited to Greece, but also occurs in part of the Balkan Peninsula, in Italy, and in most of the islands of the Mediterranean from the Grecian Archipelago to the Balearic Islands, as well as in parts of Asia Minor and Syria.

Testudo ibera.

The Moorish or Iberian Tortoise, *Testudo ibera*, is very similar to the first-mentioned species. It attains, however, a larger size; old females being eight or nine inches in length. It is distributed in Morocco and Asia Minor, extending into Persia. It also occurs in certain parts of Southern Andalusia, but it may have been introduced into the last-mentioned region from Morocco. The following differences between these two species may be briefly noticed:—In *Testudo graeca* the posterior shield of the carapace is divided in the middle line. In *Testudo ibera* there is no apparent dividing line. In *T. graeca* the fifth neural shield is much broader than the anterior shields. In *Testudo ibera* it is not usually broader, but narrower. In *Testudo graeca* the scales on the anterior surface of the forelimbs are small, and are arranged in six to ten rows. In *Testudo ibera* the scales are large and imbricating, and form only four or five rows. In *Testudo graeca* the posterior surface of the thigh is smooth; that of *Testudo ibera* has a large, horny, conical process or tubercle. The older specimens of *Testudo ibera* may also be distinguished by the posterior part of the plastron being flexible, as on a rudimentary hinge, and it is thus rendered slightly movable; this is more especially the case in the females.

An account of the habits of these tortoises has been given by Gadow and by F. and G. Rumpf. The very frequent occurrence of the tick, *Hyalomma syriacum*, Koch, on the limbs, &c., may here be mentioned.

External Characters.

The parts seen superficially are the head, neck, dorsal carapace, ventral plastron, limbs, and tail. The head is narrow anteriorly, broader behind the eyes, narrower again further posteriorly, and then passes gradually into the neck, which has considerable power of extension and retraction, through the action of well-developed protractor and retractor muscles. On the surface of the head small scales are situated, the external nares at the anterior end, and the eyes laterally. The tympanic membrane is not clearly differentiated from the ordinary skin of the head, the tongue is not protrusible, and the upper and lower jaws are devoid of teeth, but each has a horny plate underneath the skin, which fits very accurately on the maxillary and mandibular bones. The

eyes, which are dark, with a brown or bluish tinge, or dark grey, have an upper and lower eye-lid, and a nictitating membrane. The carapace is oval, and very convex; it is narrowest from side to side at the anterior end, broader at the middle of its length, and broadest a short distance from its posterior extremity. The carapace and plastron attain a considerable thickness, and the size of the body is remarkably decreased, when these are removed. The horny, epidermic shields overlying the bony plates are easily peeled off after moistening their surfaces with boiling water, and the subsequent addition of acid readily dissolves away the calcareous material of the latter, which then have a leather- or rubber-like consistency, and can be easily removed in a somewhat similar manner to peeling off the skin from an orange. When the carapace and plastron are removed in this manner, and the lungs perforated, one has a relatively long, soft, flattened animal, which can be dissected either from the dorsal or the ventral surface.

By the former method only can one follow satisfactorily the distribution of the spinal nerves, and more especially that of those arteries and veins which are situated on the immediate internal surface of the carapace. It is, however, recommended that this, as well as the usual method of dissection from the ventral surfaces, be followed on different specimens.

The horny, epidermal shields which cover the surface of the carapace and plastron, external to the bony plates, do not exactly correspond with the latter, either in number or position; they are already fairly hard in a specimen only six weeks old, definitely harder than the bony plates, and they develop more rapidly than the latter.

Shields of the Carapace (*Pl. 19, figs. 1, 3, 5*).

The carapace has the following arrangement of horny shields:—

The median series, consisting of:

1. Five large neural shields, a small nuchal shield anteriorly, and a large pygal shield posteriorly.
2. Four costal shields on each side of the neural shields.
3. Lateral to the costal shields, eleven pairs of marginal shields, excluding the anterior or nuchal shield and the posterior or pygal shield.

Shields of the Plastron (*Pl. 19, fig. 2*).

The plastron has six pairs of relatively large shields and two small shields, laterally and anteriorly, and one small shield, laterally and posteriorly, on each side at the junctions of the carapace and plastron.

The large paired shields in their order, in the antero-posterior direction, are the gular, humeral, pectoral, abdominal, femoral, and anal shields. The small shields at the junctions of the marginals with the plastron are the

axillaries, situated antero-laterally, and the inguinals, postero-laterally. In *Testudo ibera,* the axillary and inguinal shields may be regarded as the last stage in the reduction of a lateral row of shields, termed the infra-marginals; in the common green turtle, *Chelone midas,* for example, there are six infra-marginals on each side.

The relative position of the epidermic horny shields and dermic bony plates of the carapace is shown in Pl. 19, fig. 3. The horny plates, when removed, are seen to be fairly translucent, but contain a fair amount of pigment. The margins of the shields leave indented markings on the underlying bony plates, which are obvious when the shields are removed. The surfaces of the shields show folds, elevations, and depressions which are produced by the mode of growth.

The skin of the Chelonian consists like that of other Vertebrata of epidermis and dermis, the first composed of the superficial stratum corneum and the deeper-lying stratum Malpighi. The stratum corneum consists, as usual, of squamous and the stratum Malpighi of columnar cells, beneath the latter there are pigment cells. The dermis has become specially developed at these areas of the skin at which the carapace and plastron are developed, and a section through this part shows an upper osseous part, and a lower leathery or connective tissue part. The shields consisting of horn-like material have already been formed during the latter part of incubation, and they are consequently already present in the young when they leave the egg, in the same number as in the adult. They develop rapidly, and independently of the bony plates. The shields of the carapace of a six weeks' old specimen of *Testudo ibera* (Pl. 19, figs. 7 and 8) are already hard and firm, the plastron is softer, and its shields are not yet very distinct. The carapaxal shields, at this age, have thin but quite definite boundaries, and a thick, granular centre, which is the starting point of growth. The little shields or areolae present when the embryo is hatched persist in the adult in a modified form. The granules in the centre disappear or become rubbed down, and the middle part of the shield becomes larger and more uniform. The shields grow, like the scales of fishes, in thickness and in surface extent; horny material is gradually added to the existing shields by the activity of the malpighian cells. If, by any means, the malpighian layer of cells is entirely destroyed, the formation of new horn is no longer possible. The growth of the shields, like that of the scales of fishes, is periodic, but it has to be remembered that the latter are dermic in origin. Gadow states that the concentric rings on the shield surfaces indicate annual increments of growth, "at least in tortoises which live in temperate zones where hibernation means a complete suspension of growth." In later years the rings like those of fishes become more irregular and less distinct, and in any case various shields from the carapace and plastron should be examined to arrive at an average. In some Chelonia the outer layer of the shields is shed. The pigment formed in the lower cells at the base of the malpighian layer usually diffuses into the shields, and produces beautiful coloration in such cases as *Chelone imbricata,* the turtle from which the familiar "tortoise shell" is obtained.

Regeneration of the Shields and Plates.

In the specimens which are used for dissection in zoological laboratories, there are many evidences of parts of the shell having been injured and subsequently repaired; there being apparently a very considerable capacity of recovery after injury, and of regeneration. When the horny or even the bony layer is injured, the adjacent malpighian cells proliferate and produce new horny material, new bone is also formed from the deeper dermic layer, and thus the break or gap in the shell is made good in a few months' time. The ordinary concentric markings are naturally, however, not present in this new deposit of horny material. In one case, it is related that one-third of the whole shell had been replaced in this manner within a year or two. It appears obvious, however, that any injury which destroys the malpighian cells and the bone-forming cells entirely, will prevent the re-development of parts of the shell.

Epidermal Hard Parts.

The horny epidermic shields are reduced in number in Testudo, as compared with that in many other thecophoran species. Other epidermic hard parts occur in the scales of the head and limbs, in the nails and the horny jaws covering the anterior parts of the mandibular and maxillary arches. The epidermic parts of the carapace and plastron are already hard, it has previously been noted in a six weeks' old specimen, and the scales on the head and limbs must be an additional protection. The scales on the limbs are sometimes sharp and pointed, and they consist of an external layer of horny matter, and a deeper nodule-like part of bony material. The nails are fairly long and project from the terminal digits of the fore and hind limbs; they must undoubtedly be efficacious when the animals are burrowing in the ground. The horny plates covering the jaws in front of the mouth have fairly sharp cutting edges, and are no doubt of use in the absence of teeth.

The Salient Structural Features.

The shell (carapace and plastron) forms the most characteristic feature of these as of all species of Chelonia; its presence and shape bring about correlative changes in many parts. When the entire animal is removed from the box or shell of the well-known shape, it is seen how admirably the body organs had been as it were packed into a relatively small space; but it is just this concentration of a comparatively large body into a relatively confined space which makes the dissection of the animal, while still enclosed in the carapace, so difficult. In tracing the nerves, arteries, and veins, one of the great difficulties is that of following them round "awkward corners."

The significance of the vertebral column in the Vertebrata as a protective, hollow, axis for the spinal cord, and as a support on which the other parts may be said to hinge, is well known, but in the Chelonia the vertebral column

has, in a sense, become subsidiary to the carapace. The trunk vertebrae have become reduced to thin compressed bones, the dorsal parts of which appear to fuse with expanded bony plates, the neural plates. The ribs also which normally protect the delicate organs of the thorax have this function taken over by the costal plates of the carapace. The iliac bones are no longer in such intimate connection with the sacral vertebrae, but more so with the costal plates. The masses of trunk muscles common in other Vertebrata are mainly reduced to traces occurring in young specimens. The function of the carapace, as a large, protective part, within which head, neck, limbs, and tail can be withdrawn, influences the development of the muscles as well as that of other organs. The neck is retracted by means of long muscles, which run from the ventral surface of the middle of the neck to a position far back within the carapace, namely, to median and posterior thoracic vertebrae. The ribs are obviously incapable of movement during respiration, and the lungs have a different position, size, and mode of action. Skin glands no longer occur; the movements of the internal organs on themselves have been reduced, and the restricted space between the carapace and plastron has modified and prevented the free movements of the limbs, so that they appear twisted; hence the name tortoise.

The physiological key words to the salient structural features are the slow rate of metabolism.

Section 2.—The Carapace and Plastron.

Bony plates of the Carapace and Plastron — Homologies of the bony plates of the Plastron—Divergent views regarding the development and evolution of the Neural and Costal Plates of the Carapace of Chelonia.

The epidermic, exoskeletal, horny shields have been described, and an account should now be given of the much thicker and stronger plates of bone, which unite together to form the osseous carapace and plastron. The carapace is in one piece, although the sutures between the different plates are persistent, as are also the junctions between the shields, the latter leaving impressions on the surfaces of the former. When the shields are removed, the differences between them and the plates in size and position are obvious.

The plastron of *Testudo ibera* is practically in one piece, except for a posterior portion, separated by a slight hinge-like part, more especially in older female specimens. The plates correspond in general, but not in exact arrangement with the shields: those of the carapace (Pl. 19, fig. 4) are as follows:—

1. A median series of neural plates.
2. A right and left series of costal plates, and
3. An external series of marginal plates.

The median series consists of an anterior nuchal, seven neurals, and two supra-caudal plates; their characteristic feature is the fusion with the under-

lying spinous processes of the vertebrae of the trunk; in *Testudo ibera* there are nine or ten; the latter, if the anterior or nuchal plate of doubtful origin is included. The plates of the carapace and plastron are mainly formed from the greater part of the thickness of the dermis, only a thin layer of connective tissue of the lower surface remaining unossified. The large anterior nuchal plate lies dorsal to the eighth or last cervical vertebra, but its posterior corner is in close connection with the neural spine of the first thoracic vertebra. There is some evidence from a comparison of the condition in other Chelonia that the nuchal plate may be of paired origin. Seven smaller neural plates are situated posterior to the large nuchal plate in direct contact with seven trunk vertebrae, and then follow two supra-caudals which are not connected with the neural spines of the anterior caudal vertebrae. "The distinction has been drawn that true neural plates are firmly fused with the spinous processes of the underlying vertebrae." The eighth and ninth plates, as shown in Pl. 19, fig. 4, have no trace of a connection with spinous processes, and may therefore be regarded as neurals which either have lost their connection with, or have never been fused with, the neural processes of caudal vertebrae. Apart from the differentiation into neural and supra-caudal plates, it may be mentioned that the central or median plates are suppressed in the sacral region in some species of Chelonia, and in those cases the costal plates of either side approximate or meet in the median line.

The costal plates, situated eight on each side, are elongated in the transverse direction of the carapace, but are shorter in the posterior region.

The marginal series consists of eleven or twelve pairs of plates; the latter number if the posterior or pygal near the median line is regarded as the last pair of marginals. The infra-marginal plates, axillaries anteriorly and inguinals posteriorly, underlie the shields already mentioned, and form a lateral connection between the carapace and plastron; the inguinals do not always occur in *Testudo ibera.*

The plastron (Pl. 19, fig 6) has four pairs of bony plates, named in their order from the anterior end, the epiplastrals, hyoplastrals, hypoplastrals and xiphiplastrals, and an unpaired entoplastral posterior to the epiplastrals. The epiplastrals are generally regarded as being homologous with the clavicles, the entoplastral with the interclavicle, and the other plastrals with the so-called abdominal ribs of other Reptilia. The plastral plates are never in direct contact with any part of the internal skeleton. Osseous processes project in a dorsal direction on either side from the hyoplastron and hypoplastron to be inserted into the substance of lateral parts of the carapace (Pl. 19, fig. 6). These processes are very liable to escape observation, as they are intimately welded into the substance of lateral plates of the carapace. During the preparation of the skeleton of a fairly young tortoise by boiling, after the horny shields have been removed, the carapace and plastron can be gradually pulled apart, and the connecting processes will then be exposed. The connection between the carapace and plastron by the infra-marginal plates and axillary and

inguinal shields may be regarded as the superficial bridge, and that just described as the infra- or hyo- and hypoplastral bridge. In the usual method of opening the shell by sawing through the more lateral parts of the plastron, these bridges are severed, and are likely to escape notice.

The various plates of the carapace and plastron can be separated from one another by prolonged maceration, when the shapes of the individual plates are well seen; one cannot but admire the way in which the plates, so variable and sometimes irregular in shape, fit into one another, the processes of the one into bays of the other, to form a united whole, reminding one of the most intricate of children's puzzles.

In previous paragraphs the positions of the epidermic shields and the dermic plates have been noticed; it remains to note some points regarding their development. It has already been stated that the horny shields, which occur in all Chelonia with the exception of the Trionychidae and the genus Dermochelys, are already present when the young are hatched, and, except that they are not so hard, are very similar to those of the adult. With the exception of the external shields and three anterior plates, the plastron is a dermal ossification; the plates of which it is composed are not preformed in cartilage. In the majority of Chelonia, the plastron consists of nine plates, but in some cases, such as Dermochelys and Stauropus, there is not an unpaired plate or entoplastron, and in others, a paired mesoplastron is interpolated between the hypoplastron and the xiphiplastron.

The anterior pair of plates (epiplastra) and the unpaired plate behind and between them (entoplastron) are generally regarded as being homologous with the clavicles and episternum respectively of Lacertilia and some other Reptilia.

Homologies of the bony plates composing the deeper part of the plastron.

It has already been noted that the bony plates of the plastron are an anterior pair of plates, the epiplastra, an anterior median plate, the entoplastron, a second pair of plates, the hyoplastra, a third pair, the hypoplastra, and a fourth pair, the xiphiplastra. In addition to these, there still occurs in some living Pleurodira another pair of plates—the mesoplastra—situated between the hyoplastra and the hypoplastra. In some genera, the paired plastral plates do not meet medianly, and consequently there is a smaller or larger fenestra, which probably represents a primitive feature. An interesting example of the occurrence of this fenestra is found in *Testudo Loveridgii*, in which large parts of the hyoplastra, mesoplastra, and hypoplastra are undeveloped medianly. It can be recognised even with the naked eye that the plates of the plastron underlying the outer epidermic shields are bony. Hoffmann made a detailed study of the histological structure of the plastral plates, both of young and more mature Chelonia, and there can be no doubt, firstly, that the plates have the same structure as

bone, and, secondly, that their mode of development agrees with that of membrane as contrasted with cartilage bone. Whatever views may be held regarding the mode of development, and the homologies of the plates of the carapace, there appears to be almost general agreement that the plastral elements do not correspond with cartilage bones, but with membrane bones in their development.

Three of the nine or eleven plates of the plastron, namely, the anterior entoplastron and the epiplastra, are generally regarded as of a different series from the hyo-, meso-, hypo-, and xiphi-plastra. When the positions and shapes of the medianly situated entoplastron and the lateral epiplastra are compared with the anterior part of the pectoral girdle of lacertilian and certain extinct saurian reptiles, a striking resemblance is observed with the membrane bones of that part, the entoplastron with the episternum or interclavicle, and the epiplastra with the paired clavicles. It cannot be dogmatically asserted that these plastral elements of the Chelonia are homologous with the clavicles and interclavicle or episternum of other Reptilia, but there is a certain element of plausibility in the suggestion.

The other series of elements or dermal plates making up the plastron, the hyoplastrals to the xiphiplastrals, are regarded as corresponding with the so-called abdominal ribs, or gastralia or parasternum, occurring on the ventral surface of the abdomen in Sphenodon and in some other recent and extinct Reptilia. The gastralia of Sphenodon, which are exposed on reflecting the skin from the ventral surface of the abdomen, consist of about twenty-five osseous parts situated successively posterior to the sternum and extending to the pelvic region, those anterior being only loosely attached to the skin, but the majority lying in close adherence with it. Each resembles a very open capital V, with the apex directed forward. Each consists of three closely associated bones—namely, a median one, forming the base of the V, and a lateral, forming the greater part on either side. A cross row of epidermal scales is associated with each of the gastralia, and two lateral parts of a gastralia on each side with the basal part of each true rib. These gastralia of Sphenodon were originally figured by Gegenbaur and Günther. They are present in most extinct Reptilian groups, with the exception of Theromorpha, in several Dinosauria, in the oldest known bird Archaeopteryx, and among recent Reptilia in the Crocodilia. In fact, the occurrence of gastralia was not rare in extinct Vertebrata; they were present, for example, in Archegosaurus and other Stegocephalian genera. It would therefore not be surprising that they should occur among recent Reptilia in the Chelonia and in a modified form.

Proceeding from the assumption that the hyo-, hypo-, and xiphi-plastrals correspond to gastralia, Hay endeavoured to answer the question, how many gastralia have been concerned in the construction of the plastron. From a comparison of forms in which gastralia occur, he was led to the surmise that the plastron of Chelonia is composed of the entoplastron and epiplastra derived from the interclavicle (episternum) and clavicles, and of a pair of hyoplastrals,

a pair of mesoplastrals in some, a pair of hypoplastrals and a pair of xiphiplastrals, thus, three or four pairs of plates corresponding to the same number of gastralia. It appears probable, too, that, as there is a large fontanelle in the median line in most young turtles, representing perhaps a primitive condition, the plates of Chelonia represent the lateral parts, not the median part, of the gastralia or other reptiles.

Hay's views concerning membrane bones are rather aberrant. He distinguishes in the skeleton of the Amniota three kinds of bones: cartilage bones, membrane bones developed from the integument (true dermal bones), and deeper membrane bones developed from the fasciae beneath the skin (fascial bones). True dermal bones are exemplified by the osteodermal plates of the scales of Scincid lizards, and fascial bones are illustrated in the abdominal ribs of Sphenodon and Crocodiles. In the alligator, Cayman, there are both kinds—namely, dermal ossifications in the scales of the skin, and fascial bones, developed underneath the skin (abdominal ribs). Sphenodon has the second, but not the first. Hay would, therefore, draw the distinction that the plates of the plastron are fascial as contrasted with dermal bones. Versluys points out that the so-called subdermal bones are not really developed beneath the dermis; he distinguishes epithecal and thecal plates.

Divergent views regarding the neural and costal plates of the carapace.

Considerable divergence of views has prevailed concerning the development of the neural and costal plates of the carapace of Chelonia. Cuvier (1799) held that the costal plates were formed by the dilatations of eight ribs of bony processes, which took their origins at the junctions of the vertebrae, and terminated at a marginal part which surrounded the entire carapace.

Gegenbaur (1898) questioned whether the ribs of the Chelonia were "not in reality enormously developed transverse processes, and considered that the neural and costal plates have developed in the integument."

Claus (1884–1885) wrote that the spinous processes of eight of "the thoracic vertebrae (2nd to 9th) appear in the middle line as horizontal plates (neural plates), the ribs of the same vertebrae are transformed into broad transverse plates (costal plates)."

Huxley (1871) stated that the neural and the costal plates existed as expansions of the cartilages of the neural spines and the ribs of the primitive vertebrae before ossification took place. This being the case, "the neural and costal are vertebral and not dermal elements, however similar they may be to the nuchal, pygal, and marginal plates."

Hoffmann's views (1890) were, briefly, that the primitive vertebrae and ribs composed of cartilaginous tissue become encrusted with bone, and that the neural and costal plates arise outside the vertebral and costal periosteum—that these plates are not expansions of the vertebrae and ribs, but are membranous ossifications immediately surrounding the vertebrae and ribs. The costal and

neural plates are dermal ossifications, which develop round preformed cartilage parts (ribs and spinous processes), and finally entirely replace them.

Haycraft (1891) criticised Hoffmann's view, in holding that the plates in question developed outside the vertebral and costal periosteum, in that "there is no true periosteum at all." The neural and costal plates were developed round neural or costal cartilages, in contrast to the plastral plates, which were never at any period connected with cartilage. The costal plates are not ribs, for the usual conception of a rib is a long cylindrical bone enclosed in a periosteum. The costal plate is a rib expansion. He held that, as there was no periosteum in the case of the turtle, ossification spread outwards, and involved the whole body wall. The neural plates were developed in a similar manner. Haycraft's views concerning ossification and the periosteum break down when the attempt is made to apply them to tortoises proper.

Hay (December, 1898) held that the marginal bones of turtles, the plastral plates, the nuchal plate, the neural and costal plates are not dermal but subdermal fascial bones. He held that in the phylogeny of Chelonia there was, firstly, a scaly skin containing osteodermal plates, and that, later, other fascial plates appeared beneath the first, which were, in course of time, transformed into the nuchal, the neural, and the costal plates. As the second set increased in importance, the first series of plates diminished. In 1908, Hay stated his opinion that the primitive Testudinata possessed a double shell—namely, a superficial layer of plates (epithecal) and a deeper layer (thecal). The Leatherback (Dermochelys) retained the superficial epithecal layer, but lost most of the thecophorous shell.

Versluys (1913) maintains that "the shell of tortoises and turtles is formed by a combination of two layers of dermal ossifications, a thecal layer and a more superficial epithecal layer, the latter generally represented by the marginals only." Proctor (1922), after a study of the bony plates of *Testudo Loveridgii*, came to the conclusion that the costal and neural plates "are dermal"—not endoskeletal—"in origin and similar in every way to the nuchal, pygal, and marginal plates, as was first suggested by Carus (1834), and was followed up by Peters (1838), Owen (1849), Baur (1887), Gadow (1899, 1905, 1909), and Versluys (1914)." A striking point of evidence in favour of this is that the costal and neural plates "are developing while the ribs and neural arches of the true skeleton are degenerating." Miss Proctor also held that there is a definite correlation between the growth of the bony plates and that of the shields.

It will thus be seen that the question of the development and phylogeny of the neural and costal plates is a very complicated one; the matter is still being re-investigated, and the last word has not yet been said on this interesting morphological problem.

SECTION 3.—THE SKULL.

The Skull from the posterior, dorsal, lateral, and ventral aspects — Foramina of the Skull—General characteristics of the Skull.

Posterior aspect of the Skull (Pl. 20, fig. 1).

The foramen magnum is surrounded by the small basi-occipital ventrally, the ex-occipitals laterally, and the supra-occipital dorsally. The occipital condyle is fairly large, and has two shallow posterior depressions for the attachment of the suspensory ligament, which extends from the anterior end of the odontoid process. A small process projects laterally on each side of the occipital condyle, slightly anterior to its posterior margin. The supra-occipital has a prominent median occipital crest to which muscles, such as the occipito-squamoso-maxillary ("temporal," Bojanus) are attached. The foramina are better studied in the larger skulls of marine turtles, in which those of the vagus, the hypoglossal, and the spinal accessory are seen perforating the ex-occipital bones. The squamosal, quadrate, and quadrato-jugal are situated on either side, external to the ex-occipital, and the tympanic recess is situated adjacent to these three bones, but is better seen from the lateral aspect. The part of the quadrate, with which the proximal extremity of the lower jaw is connected, is easily observed, and the quadrato-jugal is situated dorsal and anterior to it. Part of the temporal fossa, which is, however, mainly situated more anteriorly, can also be seen from the posterior aspect; it is bounded medianly by the parietal and anteriorly by the post-frontal. A small portion of the opisthotic bone, the exact position of which is better seen from the dorsal aspect, appears lateral to the ex-occipital on either side. All the bones mentioned above, with the exception of the basi-occipital and supra-occipital, are paired bones.

Dorsal aspect of Skull (Pl. 20, fig. 2).

On the median, dorsal surface of the skull, the following bones are situated in their order, commencing posteriorly: the supra-occipital, parietals, frontals, pre-frontals, and pre-maxillae. The occipital crest is continued forward beyond the lateral part of the supra-occipital, so as to lie between the parietals. In the depression at the side of the supra-occipital, the opisthotic is situated posteriorly and the prootic anteriorly. The squamosal lies lateral to the opisthotic, and the articular part of the quadrate is situated ventrally and anteriorly to the first named. At the anterior, lateral part of the prootic, there lies a small bone, between it and the pterygoid process; it has been suggested that this corresponds with the ectopterygoid of fishes, but its homology is doubtful. The upper part of the quadrate, which is situated dorsal to the tympanic recess, is lateral to the so-called ectopterygoid. The quadrato-jugal lies anterior to the quadrate, and forms a large part of the lateral wall, or arcade, of the temporal fossa, the anterior boundary of which is formed by the post-frontal.

The jugal proceeds in an oblique ventral direction from the anterior end of the quadrato-jugal to meet the maxilla, at the anterior end of which is the pre-maxilla. At the posterior region of the skull part of the ex-occipital may come into view on either side, medianly and ventrally to the opisthotic.

Lateral aspect of the Skull (Pl. 21, fig. 1).

A deep valley-like depression is situated between the supra-occipital and parietal medianly and dorsally, and the squamosal and quadrate laterally. The floor of this depression consists mainly of the opisthotic and prootic, which are not, however, seen when the skull is viewed from the side. The tympanic cavity, which is situated further lateral, is bounded posteriorly by the squamosal, and dorsally, medianly, and ventrally by the quadrate. During life, the tympanic membrane extends across the external opening of the tympanic cavity, and an extra-columella externally and a stapes internally extend across the cavity of the middle ear to the fenestra ovalis, see Section 12; the latter is readily seen in the dried skull. The opisthotic forms the posterior and part of the upper and medial boundary of the auditory labyrinth, and the prootic also takes part in forming the upper and medial parts.

In the lateral view of the skull three cavities are obvious, namely, the temporal fossa, the tympanic cavity, and the orbit. The medial bones, supra-occipital, parietal, frontal, pre-frontal, and pre-maxilla are partly seen. The upper jaw is formed by the pre-maxilla and maxilla; on each side there is a large supra-temporal fossa, which is bounded medianly by the anterior part of the parietal, anteriorly by the post-frontal, laterally by the quadrato-jugal and quadrate, and posteriorly by the prootic and the so-called ectopterygoid already mentioned. The arcade is formed by the post-frontal, quadrato-jugal, and quadrate. On the ventral aspect the temporal fossa is bounded by the pterygoid medianly, and by the more lateral bones as noted on the dorsal surface; it is separated from the orbit by the post-frontal. Lastly, in the lateral view of the skull, the occipital condyle, par-occipital processes, and ex-occipitals are seen posteriorly.

Ventral aspect of Skull (Pl. 21, fig. 2).

The following bones are seen in a ventral view of the skull commencing posteriorly: part of the dorsally situated occipital crest, anterior and ventral, to which follow the occipital condyle, basi-occipital, basi-sphenoid, pterygoids, palatines, with the vomer medianly between them, parts of the maxillae, and the pre-maxillae.

The basi-occipital apparently does not take much part in bounding the foramen magnum, the greater part of the latter being formed by the ex-occipitals, and the supra-occipital. The basi-occipital and the ex-occipitals apparently both take part in forming the single occipital condyle. A small process situated slightly anterior to the posterior margin of the condyle, and adjacent to the junctions of the basi-occipital with the ex-occipitals, passes straight out

in a lateral direction; these may probably be termed the par-occipital processes. The basi-sphenoid is larger than the basi-occipital, and its anterior part is concealed by the pterygoids meeting in the middle line. The pterygoids are the largest bones on the ventral surface of the skull; they are separated from each other posteriorly by the basi-sphenoid; they meet in the median line anteriorly and are continued into a process posteriorly and laterally, which is situated between the quadrate, basi-occipital, and ex-occipital. The presphenoid, which in the mammalian skull lies in front of the basi-sphenoid, is covered over in Testudo by the pterygoids meeting in the middle line. The palatines are situated in front of the pterygoids with the unpaired vomer between them. The palatines have two lamellae, which, in conjunction with the vomers, form the canal between the nasal cavity and the mouth, the internal openings of which are the choanae. The upper jaw is formed anteriorly by the pre-maxilla, and laterally by the maxilla; these bones are covered over during life by a horny plate which fits very exactly over them; the lower jaw is similarly invested by a horny plate. The jugal is seen posterior and dorsal to the maxilla; it passes posteriorly in a dorsal direction to the anterior end of the temporal fossa. At the posterior and lateral part of the skull, the large articular surface of the quadrate appears from this point of view, and the squamosal and opisthotic posterior to it.

The hyoid plate in *Testudo graeca* consists of a broad, median part, which is mainly cartilaginous, with a medial fenestra covered over by connective tissue; two pairs of lateral horns spring from the median part (Tafel, xviii, fig. 4, Hoffmann). In the ordinary method of macerating the skull, it is difficult to keep the hyoid intact, and therefore it is better to remove the part previously and macerate it separately from the rest of the skull.

The lower jaw consists of six bones on each side. The cartilaginous foundation of the lower jaw, Meckel's cartilage, persists more or less throughout the life, and this is more especially the case in the marine genera. Meckel's cartilage has, however, more connective tissue than cartilage cells. The dentary is the largest bone of the lower jaw. In the young Testudo there is a connective tissue and cartilaginous connection between the two halves of the lower jaw, but this tends gradually to disappear in successively older animals. The articular, by means of which the lower jaw is attached to the quadrate, is the continuation of Meckel's cartilage; it is situated at the posterior boundary of the lower jaw: on the inner upper surface of the latter is the opercular and the angular posterior to it. The opercular forms the medial boundary of Meckel's cartilage, which then runs further in a groove of the dentary, and becomes exposed. The supra-angular is situated posteriorly on the external surface of the lower jaw and the complementare anterior to it, partly on the external, partly on the internal surface of the former; it is continued dorsally into a process, the coronoid process.

Foramina of the Skull.

The foramina are better examined in a larger skull, such as Chelone (Pl. XV, xviii, Hoffmann). The following may be noted:—Each ex-occipital is perforated by a canal for the hypoglossal nerve, and at its anterior, internal margin adjacent to the prootic is the internal foramen for the vagus and spinal accessory nerves. The vagus and spinal accessory nerves run in a sulcus on the upper surface of the ex-occipital towards the exterior. The foramen externum for the vagus and spinal accessory is situated on the external surface of the ex-occipital. The ostium superius ductus carotidis externae (Bojanus), which communicates with the temporal fossa, is situated on the dorsal surface of the prootic, and on the anterior part of the medial surface of the latter there are three small apertures closely approximated to each other, namely, an oval and two rounded apertures. The oval aperture is the foramen for the facial nerve, the anterior, rounded aperture that for the vestibular branch of the auditory, and the posterior rounded aperture that for the cochlear branch. The foramen for the glossopharyngeal nerve is situated on the posterior part of the medial surface of the prootic. The sphenoidal foramen (Bojanus) is a large, more or less oval aperture for the supra-maxillary and infra-maxillary branches of the trigeminal nerve; it occurs between the anterior internal margin of the prootic, the lateral bone (ectopterygoid), the pterygoid, and the descending process of the parietal. The sinus cavernosus is bounded partly by the prootic and partly by the pterygoid, basi-sphenoid, and lateral bone. Into the sinus cavernosus opens a canal, the internal opening of the canal for the artery carotidis cerebri and sympathetic branch of the palatine nerve. The internal opening of a second canal occurs above the internal opening of the first canal mentioned, and opens similarly into the sinus cavernosus; it is formed by the prootic and the ectopterygoid. This second canal is for the facial nerve, which after perforating the prootic, runs posteriorly and outwards, and leaves the cavity of the skull by the large opening, which is situated at the posterior part of the skull, and which is bounded by the quadrate, pterygoid, basi-occipital, and opisthotic. The external carotid artery, the internal jugular vein, and the palatine branch of the facial (partially) also pass through the same canal as the main branch of the facial. The foramen ovale, to which the columella auris passes from the tympanum, is situated in the internal wall of the middle ear or tympanic cavity. The optic foramen is situated in the partially calcified connective tissue, which represents the orbito-sphenoid. The external opening of the canal for the artery carotidis cerebri and for the sympathetic branch to the palatine nerve is situated at the posterior margin of the posterior and lateral continuation of the pterygoid, which appears between the quadrate and the basi- and ex-occipital. The naso-palatine foramen is adjacent to the pre-maxilla, palatine, and pre-frontal.

General Characteristics of the Skull.

The skull in some respects resembles that of Sphenodon and that of the Crocodilia, but presents special features. The following points may be mentioned as salient features of the skull of Chelonia. As negative features may be noticed, the absence of separate lacrymal bones, of clearly defined ossa transversa, of an inter-parietal or pineal foramen, and of nasals. The unpaired vomer aids the palatine in forming a septum between the choanae. The palatines and pterygoids form a continuous roof to part of the mouth; the latter bones diverge posteriorly, and are suturally connected with the quadrate, opisthotic, basi-occipital, and basi-sphenoid. The basi-sphenoid appears between the basi-occipital and the diverging pterygoids. The quadrate is firmly attached, and hemmed in on all sides by the adjacent bones; it is placed almost vertically, and has a large articulating surface for the lower jaw. Within the tympanic cavity there lie an extra-columella externally and a stapes internally. The quadrate is partially overlaid by the squamosal. The jugal by connecting with the maxilla aids in the formation of the posterior rim of the orbit.

Section 4.—The Vertebral Column.

Cervical vertebrae—Dorsal vertebrae—Sacral vertebrae—Caudal vertebrae.

The vertebral column of *Testudo ibera* has eight cervical, ten dorsal (including two sacrals), and about seventeen caudal vertebrae.

The eight cervicals are free from the carapace; the dorsals (ninth to eighteenth vertebrae, inclusive) attached to it, and the caudal vertebrae are free.

Cervical Vertebrae (*Pl. 20, figs. 9, 10, 11; Pl. 21, figs. 3–5; Pl. 22, figs.* 1–8).

When the neck is retracted, the cervical vertebrae are more or less grouped into two sets, namely, the first to the fifth, inclusive, which together form an approximately straight line, and the sixth to the eighth an obliquely curved line passing in a dorsal direction to the carapace. As is well known, the tortoise has considerable powers of protracting and retracting its head; this is accomplished by altering the curvature of the neck and cervical part of the vertebral column by means of the muscles; in the protraction of the head, in the cryptodirous genera such as Testudo, the curve of the cervical region becomes straightened out in the vertical plane. In Pleurodirous genera, such as Pelomedusa, the neck on retraction is bent sideways under the carapace. The centra of the cervical vertebrate of Testudo are well developed both as regards solidity and length, and, as they are longer than the arches, there are comparatively long intervertebral spaces between the arches of successive vertebrae. Neural spines or spinous processes are not well developed in these vertebrae; they are practically absent from the second to the sixth, and are minute in the seventh and eighth. With the exception of the atlas, the centra are pro-

longed medio-ventrally into a thin ridge (hypapophysis), which is spine-like in the case of the seventh and eighth vertebrae.

The ossification of the centra always takes place independently of the neural arches, and they remain separate for a considerable period; a suture still persists between them in the adult. True ribs, originating at the junction of the centra with the neural arches, are present from the second to the eighth vertebra, inclusive. The articular processes on the neural arches, pre- and post-zygapophyses are well developed from the third to the eighth vertebra, inclusive, the former facing dorsally and internally, the latter ventrally and externally, the shape of the articulating surfaces of the centra of the individual vertebrae varies; there are procoelous, amphicoelous, opisthocoelous, and biconvex centra (see under separate vertebrae). The notochord persists to some extent at least even in relatively old specimens.

The Individual Cervical Vertebrae.

The first vertebra or atlas is, as usual, very different from the other cervicals; it has a small medio-ventral partially bony part, representing a portion of the centrum, but the greater part of the latter is attached to the anterior end of the centrum of the second vertebra, forming a prominent odontoid process. A distinct cartilaginous suture separates the ventral part of the atlas from the slightly ring-like neural arch. The arch has a large posterior dorso-lateral process on either side with a broad articulating surface (post-zygapophysis) for the pre-zygapophysis of the following or axis vertebra. A minute, lateral protuberance is situated more ventrally on either side of the arch, which apparently does not articulate; it corresponds in position to the ribs of the other cervical vertebrae. The neural arch is apparently not completely ossified in the medio-dorsal line, for in a macerated atlas a minute space intervenes, which must either have been filled in by connective tissue or cartilage. A partially ossified cartilaginous septum (ligamentum transversum) extends across the neural cavity, dividing it into two, namely, a small ventral and a much larger dorsal space; into the former, fits the odontoid process, and through the latter passes the anterior part of the spinal cord. The odontoid process is represented by a large bony process, the posterior end of which is separated by a suture from the anterior end of the axis vertebra; its anterior end, after passing through the lower part of the canal of the atlas, projects as a more or less smooth, rounded, articulating head which fits very accurately into the pitted concavity of the occipital condyle. In most Chelonia the posterior surface of the odontoid process is movably connected with the atlas. The development of the odontoid process shows clearly that it represents the principal part of the body of the atlas, for in the embryos it has precisely similar relations to the notochord as the centrum has in the other cervical vertebrae. A chord of connective tissue passes from the anterior end of the notochord to the occipital condyle, and a fibrous band, the accessory ligament, also extends from the lateral part of the neural arch and holds the odontoid process in position.

The axis vertebra or epistropheus has an elongated centrum separated by a suture from the corresponding neural arch; the latter is much shorter than the former, leaving a large gap between the arches of the second and third vertebrae. At the junction of the centrum with the neural arch, there is a small transversely directed process on either side, which represents a rib. The centrum has a distinct keel-like ridge (hypapophysis) on the median, ventral surface. The pre-zygapophyses are situated anteriorly on the neural arch, and similarly the post-zygapophyses posteriorly. A minute spinous process is present anteriorly in the medio-dorsal line. The more or less flattened surface of the odontoid process articulates with a fairly flat surface at the anterior end of the centrum of the axis; the posterior surface of the latter is concave, the odontoid process narrows considerably anteriorly as already mentioned to form a peg-like part, which passes through the lower canal of the atlas to articulate with the hollowed surface of the occipital condyle, and there is a connecting ligament between them.

The third to the seventh vertebrae, inclusive, resemble one another fairly closely, differing only in such minor points as the shape of the centra; the eighth vertebra is, however, strikingly different from the remainder. The individual centra increase in length in the antero-posterior direction to the fifth, inclusive, but those of the sixth, seventh, and eighth are shorter. The anterior surface of the centrum of the third vertebra is convex; its posterior surface concave, the pre- and post-zygapophyses and ribs occur as usual, but not the neural spine. The hypapophysial spine is represented by a ridge.

The fourth cervical vertebra differs from the third in the centrum, being convex on both the anterior and posterior surfaces; a prominent hypapophysial ridge is present, but, as in the last, no neural spine. The pre- and the post-zygapophyses are very large, and a rib is present.

The fifth is a shorter vertebra than the preceding; its centrum is slightly bi-concave (two concavities separated by a median ridge) anteriorly, and slightly bi-convex (two convexities separated by a median ridge) posteriorly. The other processes occur as in the previous cervical vertebrae, but from this vertebra (fifth) to the eighth the articulating processes become much stronger, no doubt in connection with the necessity for modification in relation to the extension and contraction of the neck.

The centrum of the sixth cervical has a slightly bi-concave, anterior surface, and bi-convex (small convexity on either side of the median line) posterior surface.

The anterior surface of the centrum of the seventh vertebra has two concavities separated in the median line by a ridge, and the posterior is similar, but in this case the concavities are more pronounced.

The centrum of the eighth vertebra has two convexities anteriorly separated in the median line by a deep groove, and a single convexity posteriorly. This vertebra differs markedly from the others in general outline. The centrum is very much shorter, a neural spine is present, the post-zygapophyses are very well developed, in relation to articulation with the first thoracic or dorsal

vertebra. Three sesamoid bones occur in connection with the fourth, fifth, and sixth cervical vertebrae.

It will, thus, be noted that the individual cervical vertebrae vary very considerably in the form of the centra, for they may be procoelous, amphicoelous, opisthocoelous, or bi-convex on both surfaces. The third vertebra may be termed opisthocoelous, the fourth bi-convex, the fifth and eighth modified procoelous, the seventh modified amphicoelous, and the eighth modified bi-convex.

Dorsal vertebrae (*Pl. 19, fig. 5*).

The ten dorsal vertebrae are attached to the neural plates of the carapace. The first thoracic or ninth body vertebra differs from those more posterior; the anterior articular processes or pre-zygapophyses are long and broad in adaptation to articulation with the post-zygapophyses of the last cervical vertebra, which are, as has been previously noted, much elongated. This vertebra is also shorter and more massive than those situated posteriorly. The anterior surface of the centrum is deeply concave, and thus adapted to the insertion of the posterior convex end of the centrum of the eighth cervical.

A rib extends from the anterior part of the centrum of the first dorsal vertebra near the junction of the first dorsal and eighth cervical vertebra to the first costal plate of the carapace. A second process or rib extends from the interval between the first and second dorsal, similarly to the first costal plate; these first two ribs converge peripherally as they enter the first costal plate. The third rib passes out between the second and third vertebra to the second costal plate. The more posterior ribs originate and pass outwards to the costal plates in a similar manner, except that the eighth, ninth, and tenth ribs come off not invertebrally but vertebrally.

The dorsal part of the scapula or supra-scapula is inserted into a space formed by the proximal parts of the first two ribs and the centrum of the first dorsal vertebra against the ventral surface of the carapace.

The centra of the second to the seventh dorsal vertebrae are elongated and compressed from side to side; they are immovably fused to the carapace, and are separated from each other by intervening intervertebral discs. Neural arches extend from the anterior ends of the centra, medianly and dorsally (more or less intervertebral in position), and the associated neural spines pass dorsally to the neural plates of the carapace. The centra of the eighth to the tenth dorsals are shorter and more curved in a ventral direction than those of the preceding dorsal vertebrae. The ninth and the tenth dorsals are the sacral vertebrae and the eighth the pre-sacral. The ribs of the posterior dorsal vertebrae are successively less intervertebral and more vertebral in their attachment, that is, they are attached slightly further posteriorly. The last pair of ribs are very thick, and are enlarged at their distal ends into two prominent boss-like prominences, which, aided by the preceding pair, afford a connection for the dorsal extremities of the ilia, the latter under the eighth costal plates.

It has, therefore, to be noticed that the anterior dorsals differ from the cervical vertebrae in the relative position of the centra and neural arches, for in the cervical vertebrae the neural arches, ribs, and neural spines are in each case in line with the centra, *i.e.*, they are vertebral in position, but in the case of the dorsals, on the other hand, these parts are usually intervertebral. In development the centra and the neural arches ossify independently, and each arch of the dorsals originates at the anterior third of the centrum of its vertebra, and develops in an anterior direction for some distance, until it comes to lie partially over the centrum of the preceding vertebra. The neural arches, neural spines, and ribs thus come to occupy a partially intervertebral position. These facts have been proved by vertical sections of young forms previous to complete ossification. The neural arches of the cervical vertebrae, on the other hand, have the normal position, and in the last dorsal vertebrae the relative positions of the centrum and neural arch have again become normal.

In young examples of terrestrial tortoises, such as *Testudo tabulata* and *Testudo græca*, the centra of the dorsal vertebrae are bi-concave and are connected with one another by large intervertebral discs of hyaline cartilage in which the notochord still remains evident; this is also the case with medium-sized specimens, but in quite old ones the centra of adjoining vertebrae are directly in contact.

Sacral Vertebrae.

The last three dorsal vertebrae, eighth to the tenth, may be termed the pre-sacral and sacral. They are much shorter than those more anterior, and the posterior two sacrals, more especially the second, have very strong ribs, which terminate, as already stated, in boss-like structures underlying the more median part of the eighth costal plate, and to this the dorsal parts of the ilia are attached.

Caudal Vertebrae.

The caudal vertebrae are free from the carapace; there are about seventeen in *T. ibera*, twenty-one in *T. græca;* the posterior four are much reduced in size, the neural arches and the processes in general having almost entirely disappeared. The centra of the caudal vertebrae are generally procoelous. The pre-zygapophyses and post-zygapophyses are, as a rule, well developed, but neural spines are absent. The centra are usually distinct from the neural arches, and in many of the vertebrae there are relatively long ribs, which are loosely attached at the junction of the centra with the neural arches.

Hoffmann has given an account of the vertebral column and ribs of other Chelonia and of the development of these skeletal parts.

Section 5.—The Limbs and Limb Girdles.

The Pectoral and Pelvic Girdles—The Fore and Hind Limbs.

Pectoral Girdle of Testudo (*Pl. 19, fig. 5*).

The pectoral girdle of Testudo mainly consists of three parts, one dorsal and two ventrals, on each side. In Testudo the scapula, which as usual extends from a ventral position in a dorsal direction towards the carapace, is longer and narrower than the two ventral elements — the coracoid and acromial process. The scapula is continued proximally into a cartilaginous part with a bony nucleus, the supra-scapula, which approximates to the carapace, at a point adjacent to the first dorso-lumbar vertebra. The scapula at its latero-ventral end forms, in conjunction with the coracoid and acromial process, the glenoid cavity for the insertion of the humerus, and is connected ventrally and posteriorly with the coracoid and ventrally and anteriorly with the acromial process, the connection being sutural in the former but not in the latter case.

The ventral section of the pectoral girdle consists, as already indicated, of a paired posterior bone, the coracoid, and a paired anterior element, but concerning the homology of the latter much divergence has prevailed; the author follows Hart in regarding it as the acromial process. The acromial process is connected at its broad medial extremity, which is closely approximate to that of the other side, by a band of connective tissue with the anterior plate of the plastron.

The posterior bone of the ventral section of the pectoral girdle, the coracoid, is the broadest bone of the three, and in its natural position there occurs at the end directed towards the median line a cartilage or simply a suture, which represents the epicoracoid. A ligamentous band is situated at the medial end of the epicoracoid, which extends anteriorly to the median end of the acromial process, and this was termed the coraco-clavicular ligament by those investigators who regarded the anterior ventral element of the girdle as homologous with the clavicle, but it is better called the acromio-coracoidial ligament (*Ligamentum acromio-coracoideum*).

Pectoral Girdle of Chelonia.—General.

It is now almost generally agreed that the dorsal part of the shoulder girdle should be termed the scapula. It had, however, been known under a great variety of designations, namely, clavicula, schlüsselbein, pars verticalis claviculae, omoplate, schulterblatt, scapula superior s. vertebralis, scapula inferior, acromium (see Hoffmann for authorities).

The suprascapula at the dorsal extremity corresponds with the *Os triquetrum* of Bojanus, the *Os surscapulare, suprascapulare, suprascapula* of Cuvier, Rathke, Pfeiffer, Gegenbaur, Parker, and Fürbringer. It is also fairly

unanimously assented that the ventral and posterior bone of the pectoral girdle should be termed the coracoid, but it has also been termed the schulterblatt, scapula, coracoid, accessorisches schlüsselbein, clavicula, and scapula inferior s. humeralis.

A decision concerning the homology of the anterior bone of the ventral part of the pectoral girdle is much more difficult. It has been described as the Furcula (Cuvier (Leçons, 1st ed.), Rudolphi, Mohring); Schlüsselbein, Clavicula (Blumenbach, Carus, Meckel, Rüdinger, and Götte); Pars horizontalis claviculae (Bojanus); Acromium or Clavicula (Cuvier (2nd ed.) and Owen); Processus acromialis (Oken, Rathke, Pfeiffer, and Stannius); Processus coracoideus (Anonymous); and Procoracoid (Gegenbaur, Parker, Huxley, and Fürbringer).

It appears to be more than probable from the results of recent investigations that the anterior part of the pectoral girdle should be regarded as the acromial process of the scapula.

The suprascapula is a cartilaginous or partially ossified part at the dorsal extremity of the scapula, which is sometimes fairly independent of the latter. The other parts of the pectoral girdle are the Ligamentum acromio-coracoideum and the epicoracoid. The latter occurs at each medial end of the coracoid, and the former extends between the acromial process anteriorly and the coracoid posteriorly on each side of the median line, and is sometimes so well developed as to fill up all the space between these two bones, except for a small opening towards the centre.

There has been divergence of opinion regarding this expansion extending between the acromial process anteriorly and the coracoid posteriorly on each side of the middle line. It varies considerably in the extent of its development. According to Gegenbaur, there is a direct connection between the ends of these two bones. When the band is large, the end cartilage of the coracoid extends into the band as a gradually thinning lamella enclosed between two fibrous plates, and terminates in connective tissue. There is a second, but much larger, part of the band appearing as cartilaginous tissue in front of the acromial process, and extending backwards to the end of the latter. When the band is shorter, as in Testudo and Emys, the cartilage is only developed at the coracoid, and the anterior part is tendinous only, and attached to the acromial process. Gegenbaur regarded this band as homologous with the Epicoracoid (*Ligamentum epicoracoideum,* Fürbringer and *Ligamentum acromio-coracoidale,* Stannius). On the other hand, Götte held the Epicoracoideum to be that part situated at the median end of the coracoid, which persists in the cartilaginous condition. Hoffmann wrote that the band which extends "from the periosteum of the coracoid or perichondrium of the epicoracoid directly into the periosteum of the clavicle" (here termed the acromial process) "is completely homologous with the band which extends between the clavicle and the coracoid in birds, and can therefore be termed the *ligamentum coraco-claviculare.*" He found that in a dozen species of Chelonia

which he investigated the epicoracoid terminated in sharply rounded edges, and did not show a direct transition into the ligamentum coraco-claviculare.

In 1924, Hart published an important paper on the development of the shoulder girdle of the Chelonia. The following points are taken directly from this paper:—

1. The epicoracoid and the ligament only appear during the later stages of embryonal development, and are not present at first.

2. Gegenbaur's view that the ligament should be regarded as a degenerate cartilaginous bridge (Ligamentum epicoracoideum), which along with the coracoid and the anterior ventral bone surrounds a central opening, is untenable.

3. The latter foramen originates secondarily through a connection being developed between the distal ends of the two primary ventral bones of the pectoral girdle.

4. The ligament does not generally contain cartilage cells, and is always sharply marked off from the epicoracoid and coracoid.

5. The grounds which formerly apparently supported Gegenbaur's view, that the anterior ventral bone should be regarded as the procoracoid (see previously), have broken down.

As regards the epicoracoid, Hart holds that it originates in ontogeny through a progressive growth of the coracoid, and has not arisen from the degeneration of an originally complete cartilaginous bridge situated between the two ventral elements of the shoulder girdle. The ligament cannot, therefore, be regarded as the *ligamentum epicoracoideum.*

Hart's final summary is the following:—

1. The primary shoulder girdle of the Chelonia is developed from one mass of mesoblast or "blastem."

2. The space or foramen between the two ventral bony elements of the girdle does not arise by tissue resorption.

3. The ligament which connects those elements is not the vestige of a more primitive cartilaginous bridge, and it is always sharply detached from the coracoid and epicoracoid.

4. The ossification of the primary shoulder girdle proceeds from different centres.

5. No demarcation occurs between the scapula and the anterior ventral element at any stage of development.

6. The anterior ventral element should be regarded as the acromial process of the scapula, the posterior ventral as the coracoid, and the ligament which connects them as the acromio-coracoidial ligament.

7. The procoracoid does not occur in Chelonia.

Pelvic Girdle—Testudo (*Pl. 19, fig. 5; Pl. 23, fig. 1*).

The pelvic girdle consists of three paired bones, the ilia passing in a dorsal direction to articulate with the sacral ribs, the ischia and pubes situated

ventrally. These three bones meet one another on each side in the acetabulum, of which the ilium forms the dorsal section, the pubis the antero-ventral, and the ischium the postero-ventral section. The obturator foramen is situated on each side between the ischium and pubis, and is partly covered over by the obturator membrane, but there is an opening through which the obturator nerve passes out from the pelvic cavity. The pubis has three parts, an anterior median process, an antero-lateral process, and a posterior part, meeting the ilium and ischium at the acetabulum. There is a cartilaginous part situated medianly between the right and left pubis, which extends anteriorly as the epipubis (*Processus pubis anterior,* syn. *abdominalis:* Bojanus), and a similar cartilaginous band also extends between the two ischia in the median line.

The epipubis is continuous, at an early stage, with both the pubic bones, and is therefore not regarded as being homologous with the cartilage ypsiloides of Urodelan Amphibia, which appear to originate independently of the pubic bones.

In contrast to the divergent views regarding some parts of the pectoral girdle, unanimity has prevailed regarding the homologies of the bones of the pelvic girdle.

Fore-limb (*Pl. 23, fig. 2*).

The humerus is considerably larger than the femur, and is remarkable for the strong development of its proximal processes or tuberosities, more especially the medial. The humerus is also remarkable for its divergent position in relation to the pectoral girdle. This divergent position is brought about by the ligament, which runs between the humerus and the scapula, being placed in such a manner that the parts which are lateral in the higher Vertebrata become medial in the tortoise, and the parts which are medial in higher Vertebrata become lateral in the tortoise.

The humerus is very thick at its distal extremity; its head is a spherical convexity articulating in the glenoid cavity. The head is separated from the part on which the processes occur by a distinct neck. The tuberosities are the medial and the lateral, but, owing to the rotation of the humerus, the names applied by different authors are unfortunately contradictory.

The lateral process (Fürbringer) or internal tuberosity is relatively smaller than the medial (Fürbringer) or external tuberosity (Bojanus and Owen), but consists of a powerful bony ridge. This ridge occurs in the proximal part of the bone, and projects laterally and ventrally. In some genera, such as Chelone, it is represented by a larger protuberance situated on the curved side (*tuberculum musculi supracoracoidei,* Fürbringer), and a smaller one more towards the straight side (*tuberculum musculi deltoidei,* Fürbringer, deltoid crest, Owen.)

The medial process (Fürbringer), external tuberosity (Owen and Bojanus) is much stronger and higher than the lateral, and extends over the proximal third of the bone, with a more or less median tendency. These two processes,

lateral and medial, are separated by a deep groove, near the condyle in the proximal curve of the humerus, *i.e.*, the *fossa intertubercularis* of Fürbringer, the *gouttière bicipitale* of Cuvier, and on the extensor side of the groove lies the "*linea musculi latissimi dorsi.*" Distal to the medial and lateral processes, the humerus becomes narrower and more cylindrical, but it becomes larger again towards its lower extremity, where it shows some traces of distinction into separate articular surfaces for the radius and ulna.

Fore-arm.

The radius and ulna are both slightly flattened; the radius is thinner and slightly longer than the ulna, extending further distally towards the carpals. The ulna has a much deeper cavity for articulation with the external condylar tuberosity of the humerus. The radius and ulna are intimately connected with each other by dense connective tissue. The radius can be at once distinguished from the ulna, as it narrows much more than the latter towards the middle of its length and is also a slightly smaller bone.

The Carpals, Metacarpals, and Phalanges.

The carpals are more or less distinctly separated into a proximal and a distal series. The proximal carpals are the large radiale or navicular, the intermedium or semilunar, and the ulnare or pisoform. The centrale is situated near the intermedium and radiale. The distal carpals are a large pre-axial representing the first and second, and supporting the metacarpals of the first and second digits and the third, fourth, and fifth carpals (the latter with a lateral process) in connection with the corresponding metacarpals. There are five metacarpals which are short and stout, except the first, and fairly similar to each other; this holds also for the phalanges of the digits, of which there are two for the first and fifth, and three for the second, third, and fourth; the terminal phalanges are encased in horn. The fifth or post-axial digit is, as is general, the smallest. The third and fourth digits are longer than the first and second, and the third the longest digit. The terminal phalanx of each digit is long, curved, pointed, and claw-like.

Anterior Limb of Chelonia in general.

The humerus of the Chelonia differs from that of most Amphibia, firstly, in its larger size, secondly, in the great development of the proximal processes for the attachment of muscles, and thirdly by its diverging position relative to the pectoral girdle, so that the lateral parts of higher Vertebrata are here medial and *vice versa*. The humerus is more plate-like in Chelone and Sphargis than in other Chelonia. As regards the distal part of the limb there are variations in the different families and genera of the Chelonia, consisting of divergences in the predominance of certain carpals, and the fusion of others.

In the second row of carpals in the genus Testudo, carpals 3, 4, and 5 form distinct bones, carpals 1 and 2 have apparently, even in young animals, completely fused.

Posterior Limbs (*Pl. 22, fig. 9*).

Thigh.—The femur is a curved cylindrical bone, which enlarges at its proximal and distal extremities. The proximal articulating surface is a large spherical head, which fits into the corresponding socket in the pelvic girdle, the acetabulum. Two slightly rounded protuberances occur at the junction of the head and median part of the femur, the large external trochanter major and the smaller internal trochanter minor. The middle part of the femur, which is nearly cylindrical in its upper part, becomes wider from side to side posteriorly, and then the bone becomes flatter before passing into the two condyles; the latter are similar to one another in size and form, and are only separated from one another by a slight sulcus.

Leg or Crus.—The skeleton of the leg consists of a stouter tibia and a more slender fibula. The tibia is more enlarged at its proximal that at its distal end, but the reverse is true for the fibula. The tibia narrows towards the middle of its length, and then gradually expands to terminate in articulation with the tarsus. The fibula, on the other hand, is only slightly expanded at its proximal end, but enlarges at about two-thirds of its length into a cylindrical part with a condyle for articulation with the tarsus.

The Tarsalia, Metatarsalia, and Digits.

The tarsus includes (*a*) a large and prominent bone, which articulates with the distal surfaces of the tibia and fibula, and probably represents the fusion of the tibiale, fibulare, and intermedium; (*b*) in connection with the posterior surface of the latter compound bone an articular tuberosity probably representing the centrale; (*c*) distal to these two are three or four other tarsals, followed by four metatarsals, and terminating digits with their phalanges of which there are two in each digit. The distal phalanges are sharp-pointed and claw-like.

SECTION 6.—THE VISCERA AND ALIMENTARY SYSTEM.

The Viscera in situ—The Alimentary Canal—The Mesenteries—The Visceral arteries and veins—The Coelom—Pleuroperitoneal cavity—The Retroperitoneal condition.

The viscera are usually exposed from the ventral surface by carefully sawing through the shell at the lateral junctions of the plastron with the carapace, and then slowly separating the membrane—the *parietal peritoneum*—which covers them and adheres to the dorsal surface of the plastron. In

separating the plastron, stout ligaments are seen passing from it to the acromial processes, and the large pectoral and abdominal rectal muscles are also partly exposed. The exposure of the viscera is facilitated when the head is kept well extended in the anterior direction.

The parietal peritoneum is a semi-transparent membrane which covers and to some extent conceals the viscera. A small right and a larger left anterior abdominal vein run longitudinally in the parietal peritoneum from the pelvis posteriorly to the liver and pectoral muscles anteriorly.

The parietal peritoneum differs from that of most Vertebrata in being readily detachable from the rest of the body wall, for, in the Chelonia, a muscular layer does not intervene between the skin, or skin derivatives, and the peritoneal membrane, though large masses of muscles are present elsewhere, more especially in connection with the pectoral and pelvic girdles and the fore and hind limbs.

The heart is clearly defined through the semi-transparent membrane in the median line, slightly posterior to the pectoral girdle. The pericardial peritoneum, as the wall of the pericardial cavity, and the transverse septum separate off the coelom into two, the pericardial cavity containing the heart and the pleuroperitoneal cavity with the other viscera. The term pleuroperitoneal is used to distinguish it from the peritoneal cavity of placental Mammalia which is separated from the pericardial cavity by the diaphragm. The pericardium and heart are situated further ventral and posterior than in fishes and urodelan amphibia, the ventral pericardial wall lies closely adjacent to the plastron, and the dorsal pericardial wall is fused to an anterior extension of the pleuroperitoneal membrane. The pericardial sac, as contrasted with that of fishes, is an independent one, and may be regarded as having slid posteriorly and ventrally, so that it has come to occupy a position ventral to the anterior part of the pleuroperitoneal cavity (see coelom in subsequent paragraph).

Fairly clear indications of the ventricle and of the right and left auricles are seen through the semi-transparent pericardial membrane, as also of the three great arterial trunks at the anterior end of the ventricle, namely, the innominate, the left aorta, and the pulmonary.

The positions of the large left and smaller right lobes of the liver are indicated through the parietal peritoneum as large swellings situated lateral to the heart and extending far posteriorly.

In the females, the ovaries, containing ova of various sizes, are conspicuous within the pleuroperitoneal cavity, and the oviducts are prominent laterally. When the ova have acquired firm, limy shells, the oviducts, with the eggs within them, cover most of the other pleuroperitoneal viscera. Irregular, yellowish, fatty masses are situated within the membrane, which vary considerably in the degree of their development in different specimens.

Exposure of the Viscera.

When the two anterior abdominal veins are ligatured about the middle of their longitudinal course through the parietal peritoneum, and cut transversely, then the remainder of the membrane, which covers the viscera, can be carefully removed. The anterior abdominal veins, one on each side, arise posteriorly from a superficial transverse vein, on the ventral surface of the pelvic region; each vein then passes anteriorly, and, after giving off a branch which passes dorsally to the liver, receives branches from the muscles of the pectoral girdle.

The Liver.

The colour of the liver is usually bluish-brown, but it varies very considerably in different specimens. It extends far posteriorly, more especially on the right side, and consists of a larger left and a smaller right lobe which are connected with each other by a median or transverse lobe lying posterior to the heart. The lateral marginal parts of both lobes curve far dorsally to fit into the curves of the carapace.

The left lobe, when viewed from the ventral surface, almost entirely conceals the cardiac part of the stomach, situated more dorsally; it has a deep ventral cleft or groove passing from the anterior nearly to the posterior extremity; this cleft is situated a little more than one-third of the distance from the median line of the left lobe. The greater part of the left lobe of the liver, as seen from the ventral surface, has an entire margin. From the same lobe, there is a dorsal or superior extension, which lies in or fills up the space formed by the ⊃-shaped curve of the cardiac part of the stomach. This dorsal extension of the left lobe may be termed the left superior lobe of the liver (Pl. 26, fig. 1).

The left lobe is continuous with a neck or isthmus, which may be termed the transverse or median lobe of the liver. This has an anterior ventral part, which is partially separated by mesentery from a posterior dorsal part. The first of these is situated anterior and ventral to the distal part of the cardiac stomach, to the pyloric stomach, pylorus, and commencement of the duodenum. The second of these lies partly anterior and partially dorsal to the distal part of the cardiac stomach, pyloric stomach, and pylorus.

The right lobe of the liver is narrower in the antero-posterior direction than the left, and is more angular than the latter at its lateral margin. It has a deep cleft, in which the gall bladder is situated, which to some extent separates off a lateral from a more median part; the lateral part has an extension passing partly in a dorsal direction, and the median part lies partially ventral, partly anteriorly and laterally to the proximal part of the duodenum.

The right lobe of the liver has also a dorsal or superior lobe, which is, however, much smaller than the corresponding one of the left. This right, dorsal lobe is also in connection with the median lobe of the liver; it is situated dorsal to the pyloric stomach, pylorus, and duodenum, and posteriorly is closely

adjacent to the spleen and pancreas. This superior part of the right lobe might also be regarded as part of the median lobe; there is no sharp line of demarcation between the right and left lobes and the median lobe of the liver. A figure of a section of the liver of *Testudo graeca* is given by Oppel (vol. iii, figs. 663, 664).

The gall-bladder (Pl. 26, fig. 1) lies embedded in the liver, near the junction of the lateral and median parts of the right lobe. The cystic duct from the gall-bladder (Pl. 30) passes posteriorly and ventrally, adjacent to the mesentery of the right lobe and over the surface of the pancreas to open into the duodenum between the anterior and median pancreatic ducts. The hepato-cystic duct to the gall-bladder runs for some distance parallel to the cystic duct, and is joined by hepatic or biliary ducts from the liver, in connection with which there is an anastomosis. The hepatic and hepato-cystic ducts then lead into the choledochic duct (common bile duct), which runs parallel to the distal portion of the cystic duct, and opens closely approximate to it into the duodenum near the more median part of the pancreas, and beside the opening of the anterior pancreatic duct.

The liver is connected, posterior to the heart, with the parietal peritoneum by very short mesenteries analogous with the falciform ligament of other Vertebrata, and in these mesenteries a large branch of each anterior abdominal vein passes to the liver. When the right and left lobes of the liver are lifted and pressed anteriorly, the stomach, pylorus, duodenum, pancreas, spleen, part of coecum, and large intestine, are exposed (Pl. 25).

The large, main portal vein (Pl. 26, fig. 2) runs transversely across the greater part of the dorsal surface of the liver; it receives a number of portal branches from the various parts of the alimentary canal (see vascular system, p. 400).

The pancreas (Pl. 25) is a long, slender, whitish or yellowish gland, with numerous thin lobelets, which is situated adjacent to the pylorus, duodenum, spleen, and coecum, and is connected with the dorsal surface of the right lobe of the liver by the hepato-duodenal mesentery. A small part of the pancreas extends anteriorly, and lies closely applied to the wall of the pyloric part of the stomach; posteriorly this is continued into the thick main lobe, which extends along the wall of the duodenum, and terminates near its distal end. From each side of the main part of the pancreas a lobe passes posteriorly to unite and form a median part, which terminates adjacent to the coecum and the spleen.

The pancreatic ducts may be most readily seen by picking away the parts of the pancreas surrounding the distal parts of the duodenum. The position of the duodenal apertures of the three pancreatic ducts and their relation to the cystic and choledochic ducts are indicated in Pl. 30.

The spleen is a rounded, but slightly flattened, red body, situated in the mesentery, supporting the large intestine or colon, closely adjacent to the coecum.

The lungs are large spongy organs, situated dorsally one on each side, and are exposed by raising the liver and alimentary canal: those of opposite sides are not far separated medianly. The other viscera which are exposed by removing the parietal membrane are the testes (in the males), the kidneys, the coils of the small intestine, the large intestine, and the urinary bladder.

The Alimentary Canal (*Pl. 25*).

When the general arrangement of the viscera has been seen, the alimentary canal is unravelled, and the sequence of its course traced from the œsophagus to the rectum. Its course is best followed, provided a subsequent detailed dissection of the vascular system is not required on the same specimen, by removing the animal entirely from the carapace. By this method, it is at once recognised that the alimentary canal is in reality much longer than would at first sight be supposed when viewed in its more or less confined position within the concavity of the carapace. An advantage of this method of dissection is that one can follow the relative positions of the parts from the dorsal as well as from the ventral surface. The cavity of the mouth is dealt with along with the respiratory system in a subsequent section. The parts of the canal are œsophagus, cardiac stomach, pyloric stomach, pylorus, duodenum, small intestine, coecum, and large intestine.

The œsophagus is narrower than the stomach anteriorly, but passes imperceptibly into the latter posteriorly. The internal surface has longitudinal folds of mucous membrane, which extend from the pharynx to the cardiac stomach, but the horny papillæ so characteristic of the turtles do not occur. The œsophagus passes insensibly into a much wider part of the canal, the cardiac stomach, which fits into the deep depression on the ventral surface of the liver. The canal then becomes much narrower, and is directed towards the right, posterior to the median lobe of the liver, forming the pyloric chamber. Immediately succeeding the latter chamber is the pylorus, which is marked out by a great reduction in the diameter and by the presence of internal valves. The passage from the stomach into the duodenum is indicated by this abrupt reduction, but distally near the posterior end of the pancreas, the duodenum is continued imperceptibly into the remaining much coiled part of the small intestine, which passes posteriorly, then medianly, and then again anteriorly, to open into the coecum near the junction of the small and large intestine.

The small intestine of *Testudo graeca* has a few fairly high longitudinal folds of the mucous membrane, which gradually decrease posteriorly, but other folds appear between them when the first have become very much reduced in height. A muscularis mucosae does not occur, and the entire length of the small intestine is apparently devoid of glands in the genus Testudo. At the junction of the stomach and duodenum there is an internal ridge in the mucous membrane, which originates near the stomach, and consists of several longitudinal folds of the membrane. At this transitional part there are numerous

mucous glands, which are more especially abundant on the surfaces nearest the stomach. The distal part of the small intestine narrows very abruptly as it passes into the more or less rounded, thin-walled, bag-like dilatation, the coecum; the opening of the latter into the large intestine, colon, or rectum is much wider. The rectum extends across the pleuroperitoneal cavity transversely, and then turns posteriorly, the most distal part lying within the arch formed by the pelvic girdle. The urinary bladder is situated ventrally to the large intestine, anterior to the pelvic girdle: the rectum opens into the cloaca, as also the urino-genital sinus, as usual (see reno-reproductive organs). With the object of reducing the text, an account of the histology of the alimentary canal, which has been given by Oppel and Hoffmann, is omitted from this work.

Mesenteries.

In the embryo, the lateral plates of mesoblast are situated, as is well known, on each side of the more ventral part of the archenteron, and these plates later form an internal layer, the splanchnopleure, which becomes adherent to the intestine, and an external one, the somatopleure, which is situated within the muscles of the body wall, with the coelom between them. In the adult, the most internal part of the somatopleure forms the parietal peritoneum, and the most external part of the splanchnopleure constitutes the visceral or intestinal peritoneum. Dorsal to the intestine, the two walls are in connection, and form the dorsal membrane. As is well known, though the viscera and intestines are frequently spoken of as being contained in the coelomic cavity, they are really outside it; for they have been, as it were, pushed against the coelomic wall, carrying it before them.

Different portions of the dorsal mesentery are known from the names of the parts with which they are connected, and the following are recognised:— the short *gastro-hepatic* mesentery, which runs between the stomach and the centre of the left lobe of the liver; the *hepato-duodenal*, which lies between the duodenum and pancreas and the dorsal surface of the right lobe of the liver; the *dorsal mesentery* proper, which suspends the coils of the small intestine to the median dorsal line of the coelom, and has anterior continuations forming the *mesoduodenal* and the *mesogaster* of the duodenum and stomach, respectively; the mesoduodenal and the hepato-duodenal are closely connected with one another, so as to appear as one, but the mesogaster is distinct from the gastro-hepatic mesentery; the *mesocolon* supports the large intestine, and the *mesovarium* and *mesotubarium* support the ovary and oviduct.

Visceral Arteries and Veins.

The visceral arteries and veins are noticed during the first day's dissection while the alimentary canal is in a fresh condition. A large gastro-epiploical artery runs along the concave side of the stomach, and sends off branches to its dorsal surface and convex margin; the left cardiac and coeliac are two

smaller arteries. Other arteries are the spleno-duodenal, anterior and posterior mesenteric, coecal, and ileo-colical arteries. These arteries vary in different specimens, but they arise in all cases from two or three main arteries situated near the origin of the dorsal aorta, which obviously correspond with the coeliac and mesenteric arteries of other Vertebrata (see vascular system).

A number of portal veins, which collect the blood from the different regions of the alimentary canal, open into the main transverse portal running across the dorsal surface of the liver. The chief portal branches are the gastric and duodenal branches of the anterior abdominals, mesenteric veins with several branches, such as splenic, ileo-colical, common intestinal, and pancreatic veins. A number of hepatic veins, which are situated close to the main transverse portal vein, then collect the blood from the liver and pass it into the sinus venosus. It may be mentioned here that the portal veins vary in different specimens.

The Coelom.

In the adults of all Vertebrata, the coelom is divided by the transverse septum into at least two compartments: the anterior or pericardial cavity containing the heart, and the posterior or pleuroperitoneal cavity containing the other viscera, the latter being, as it were, pushed into its wall. In Elasmobranch fishes for example, one is specially familiar with the fact that the transverse septum is situated posterior to the heart, and that it divides the coelom into these two parts—the pericardial coelom anteriorly, the pleuroperitoneal cavity posteriorly. The posterior face of the transverse septum is clothed by the parietal peritoneum, and the anterior surface by the pericardial peritoneum. The liver is attached to the septum by the coronary ligament, which is really a part of the transverse septum. "In its early development, the liver is enclosed in the transverse septum which then narrows around the anterior end of the liver and forms the coronary ligament."

In the Chelonia, the relative position of the pericardial to the pleuroperitoneal cavity is altered as compared with that of fishes. The pericardial cavity has descended posteriorly, so that it comes to lie posterior to the anterior part of the pleuroperitoneal cavity; the transverse septum being no longer vertical, as in the fish, but oblique. The anterior part of the lungs now occupies the space which, in consequence of the descent of the pericardial cavity, lies dorsal to the latter. The anterior part of the lung is dorsally in contact with the ventral surface of the carapace, but ventrally the parietal peritoneum passes underneath it, so that the lung is really outside the parietal peritoneum; it is therefore said to be retroperitoneal. The posterior part of the lung, however, projects like the other viscera into the pleuroperitoneal cavity, and is covered by the parietal peritoneum.

The change in the relative positions of the pericardial sac, transverse septum, and pleuroperitoneal cavity is explained as follows.

As the heart descends, it carries with it the transverse septum and the parietal pericardium. The latter separates from the body wall, to which it is attached in fishes, and thus the pericardium becomes a free sac. The separation of the pericardial sac is helped by the forward extension of the pleuroperitoneal cavity. In other words, while the pericardial sac descends behind, the pleuroperitoneal cavity advances in front. The pericardium thus comes to be situated ventrally to the anterior part of the pleuroperitoneal cavity. The posterior wall of the pericardial sac is still the anterior face of the transverse septum, and the posterior surface of the latter is still situated, as in lower Vertebrata, between the pericardial sac and the liver. The transverse septum in the Chelonia thus forms part of the partition between the pericardium and the pleuroperitoneal cavity, the remainder of the partition arising from the rest of the parietal pericardium.

For more complete facts regarding the divisions of the coelom in the various Vertebrata, one may allude to Hyman's series of five figures, from which fig. 2, Pl. 36, has been reproduced in the present memoir, by kind permission of the author and publishers.

Section 7.—The Vascular System.

The Venous System—The Arterial System—The Structure of the Chelonian Heart—The Lymphatic System—The Ductless Glands. (Pls. 25–37).

The heart has two auricles and one ventricle, the latter with an incomplete septum. The septum between the two auricles is solid and complete, and, as it extends further down than in the Amphibia, it not only completely separates the two auricles from one another, but leads to the division of the originally single atrio-ventricular aperture into two. The left auricle is smaller than the right, and its position seems subordinate to that chamber, for the posterior and dorsal part of the right extends over the left. The pulmonary veins combine into an extremely short common pulmonary which opens into the left auricle, at a non-valvular aperture. The sinus venosus, situated on the posterior dorsal surface of the heart, is not exactly median, but is placed slightly laterally. The general form of the body has apparently an influence on the form of the heart for corresponding with the form of the body which is relatively compressed in a dorso-ventral direction especially as seen when removed from the shell, the ventricle is strikingly broad and flat, and the surface directed towards the plastron is flattened as contrasted with the arched outline towards the carapace. When the heart is viewed from the ventral surface, the bases of the principal arteries, which are exposed on clearing away the lymph sinuses and connective tissue, are, in the direction from the right hand side of the specimen towards the left, the innominate, the left aortic arch, and the common pulmonary artery (Pl. 32, fig. 1). When the heart is slightly raised the innominate is seen to be a

ventral branch of the considerably more dorsally situated right aortic arch which is concealed from view ventrally. The nature of the blood in these three vessels, the right aortic with its innominate branch, the left aorta, and the common pulmonary, is indicated in Pl. 31, figs. 1, 2, and Pl. 32, fig. 1; the innominate and right aortic arch contains arterial blood which has come from the left dorso-lateral side of the ventricle (*cavum arteriosum*), the left aortic arch has partially venous blood which passes from the right dorsal side of the ventricular cavity (*cavum venosum*), and the common pulmonary artery conveys venous blood from the right ventro-lateral side of the ventricle (*cavum pulmonale*) to the lungs (see the structure of the Chelonian heart). The right and left aortic arches and the pulmonary are really parts of the conus arteriosus which has become divided into three vessels which twist round one another in a right-handed spiral: the conus having been incorporated into the arterial system. On raising the ventricle, by cutting through the ligament attaching it to the posterior pericardial wall, and pressing it anteriorly, the sinus venosus is exposed as also the large systemic veins, which open into it, namely the right and left anterior venae cavae and the posterior vena cava with the hepatic veins. The pulmonary veins which convey oxygenated blood to the left auricle are seen at a later stage of the dissection.

Anterior Abdominal and Pelvic Veins.

On removing the plastron, a large left and a smaller right anterior abdominal vein are seen running on the ventral parietal peritoneum from the pelvic region posteriorly to the liver and pectoral region anteriorly, and at intervals during their course these veins receive minute lateral branches from the body wall and plastron. The anterior abdominals vary considerably in size, and even in distribution in different specimens. Posteriorly in the pelvic region they are connected with one or two transverse vessels, into which run a number of superficial pelvic veins from the muscles, etc., in connection with the ventral surfaces of the pubes, ischia, and thigh. Anteriorly, each anterior abdominal vein sends off a branch which passes in a dorsal direction to the liver, and then receives slightly more anteriorly pectoral, brachial, and intercostal branches.

The superficial pelvic veins convey the main posterior and median supply of the blood to the anterior abdominals, but the latter also receive blood from a lateral, as well as from a dorsal, source, the latter by a large branch of the common iliac.

The median superficial pelvic veins vary very considerably in different specimens: the extent of this variation is to some extent shown in Pl. 28, fig. 2. There may be one or two transverse vessels, and these may or may not be connected by longitudinal vessels. The strength and size of these superficial pelvics is exaggerated in a drawing of an injected specimen (Pl. 28, fig. 1).

When the vein forming the anterior transverse bridge is traced in a lateral direction towards the margin of the carapace, it is seen to be formed of several

branches; firstly, of a vessel which is in connection with a longitudinal vein which runs in an antero-posterior direction within the marginal plates—the epigastric or common longitudinal marginal; secondly, of several fairly ventral branches from the carapace (carapaxal); and thirdly, of a vessel which comes from a much more dorsal position, and is continuous with the common iliac vein (Pl. 27, fig. 1); this third vessel is later seen to consist of or to receive three chief component parts: (1) a main vessel coming forward from the more posterior parts, (2) vessels from more dorsal parts of the carapace, and (3) a branch connection with the kidney. By the first of these vessels—the epigastric—the anterior and posterior parts of the carapace are placed in connection. The anterior abdominals like the pelvics vary in different specimens, thus in one (Pl. 28, fig. 2) the right anterior abdominal does not connect posteriorly with the transverse bridge on the pelvis but curves dorsally anterior to that, and passes into the right lobe of the liver, consequently the left anterior abdominal collects the blood from both sides by the superficial pelvic veins. A small vein from the posterior part of the liver sometimes joins the lateral pelvic after this has received the epigastric and carapaxals. The pelvic bridge is joined by a bifurcate vein from the external surface of the thigh—the crural—posteriorly previous to the origin of the anterior abdominals.

Following the course of the abdominals anteriorly they are seen to receive pectoral branches from the pectoral muscles, brachial vessels from the fore-limb, and important vessels which curve round the lateral margins of the carapace and communicate by an anastomosis with a vessel running transversely in the curve of the carapace, the transverse intercostal vein, and through the latter with the common anastomosing branch of the transverse intercostals, to connect further dorsally with a longitudinal vein running on either side of the vertebral column, the azygous or common descending intercostal vein. This connection may be regarded as the anterior or pectoral link with the veins of the carapace, but there is another connection with the carapace still further anterior, namely, by the jugular. The cross in Pl. 27, fig. 1, Pl. 28, fig. 1, indicates the position of the pectoral connection.

The right anterior abdominal differs from the left in receiving a small vessel from the connective tissue immediately within the plastron, which runs in a ventro-lateral direction relative to the heart.

The Iliac and Renal-portal Veins (Pl. 29, fig. 1).

The common iliac vein, which has already been mentioned, in connection with the pelvic and anterior abdominal veins, is situated much more dorsally than those, and lies between the ilium and the carapace. It receives femoral and sciatic veins from the leg, and connects with a branch, the circumflex iliac situated more dorsally, and with vessels from the posterior part of the carapace (*posterior carapaxal*) and caudal veins from the tail. It is also in direct connection with several more dorsal veins, forming an anastomosis on the dorsal

pelvic muscles and posterior part of the carapace. The latter vessels on the dorsal pelvic muscles are also in connection with slightly more anterior vessels of the carapace, which lead into the external renal portal vein. The common iliac vein bifurcates into two vessels, one of which passes in a more ventral direction, and becomes the pelvic, and the other takes a more dorsal course, and becomes the external renal portal.

The pelvic, after receiving the more superficial veins already mentioned as coming from the carapace (epigastric and several small carapaxal veins), proceeds medianly, and connects finally with the anterior abdominal of that side through the transverse pelvic vein. The external renal portal vein receives branches from transverse intercostal veins, from the common anastomosing intercostal vein, and from the common descending intercostal or azygous vein. These communicating veins, "rami-communicantes," form connections between the veins of the carapace and the posterior and external renal portals. Further posterior, these rami are also in connection with the veins to the common iliac.

The external renal portal or dorsal branch of the common iliac, it is important to notice, has a connection with the medial azygous vein, a connection which was observed long ago by Bojanus. The external renal portal, after receiving those various carapaxal vessels, passes anteriorly to the ventral surface of the kidney, and breaks up into a number of branches, which are closely connected with the branches entering it from the following vein. The posterior renal portal is formed by an anastomosing series of veins from the gonads and their ducts, the bladder, rectum, pelvis, and cloaca. It receives a branch from the common anastomosing intercostal vein of the carapace, and is also in connection with carapaxal veins entering the common iliac.

A third vessel which is connected with the kidneys is the anterior renal portal. This vein descends from the azygous vein (posterior cardinal), situated on either side of the vertebral column; it originates near the last transverse intercostal vein (marked with a cross in Pl. 27, fig. 1), and passes ventrally towards the dorsal surface of the kidney in a tortuous course.

The dissector will probably find that his dissection of these veins does not agree with the description given here, for all these veins vary very considerably in different specimens, and they are not always the same on the right and left sides of the body.

As a general fact it should be noticed, firstly, that blood from the leg, tail, and more posterior part of the carapace may pass either into connection with the anterior abdominal and thence to the liver, or to the kidneys; secondly, blood from part of the carapace slightly more anterior may either course to the liver by the epigastric, pelvic, and anterior abdominal, or pass by the anterior renal-portal veins to the kidneys, from which it passes to the inferior vena cava.

It is also important to note the pelvic connection of the anterior abdominal with veins of the carapace, as previously stated, and the pectoral connection, by means of an anastomosis of pectoral branches, of the anterior abdominals,

and also with the azygous through a branch of the jugular vein (see later). The description of these posterior veins differs in some points from that of Nicolai on *Emys europa,* who, unfortunately, gave no figure, but the general points are similar. The description can also be correlated with the figures by Bojanus, but the latter did not describe or figure the relationships of the veins to the kidneys. The apparent differences are to some extent only those of nomenclature. Bojanus shows a large vein, which he terms the supra-renal (indicating its position above the kidneys), arising from the azygous vein, and proceeding in a ventral direction; this vein corresponds with the anterior renal portal of Nicolai. Bojanus shows a connecting vessel between the supra-renal or anterior renal portal and a transverse intercostal, which I have also observed, and also a connection with the "spermatic vein" (of Bojanus) (*i.e.,* posterior cana cava): the latter connection I have not seen, and it is more than probable that there is only an indirect one between these two veins through the kidney. Bojanus figures as the hypogastric, a vein which obviously corresponds with the posterior renal portal. A striking difference is that Bojanus shows a posterior connection between the two vessels which I term the posterior and external renal portals. The specimen from which I have taken this description was injected from the anterior part of the hind limb, and consequently the veins lying more posteriorly were not so clear, but I have taken figure 2, Pl. 29, in a modified form from a figure by Bojanus. Before leaving the subject of the posterior veins, it is important to realise that from the common iliac we have the posterior link with the veins of the carapace: the anterior link has already been indicated.

Another figure by Bojanus shows vessels which apparently correspond with the external renal portal and the common iliac veins, but the relationships are not very clear.

The Veins of the Carapace (Pl. 28, fig. 1).

The arteries and veins in close association with the carapace are exposed by removing the superficial horny shields and then carefully dissolving away the underlying bony plates with hydrochloric or other acid. The veins are more conspicuous than the arteries, but as a rule they run concurrently, the former lying superficially to the latter. There are three main pairs of longitudinal veins, commencing in order from the median dorsal surface; they are the common descending intercostal, or azygous veins, the common anastomosing branch of the transverse intercostals, and the longitudinal marginal vein or epigastric. There is apparently confusion about these three veins. The first here retains the name given to it by Bojanus (vertebral of some authors); the second is also the name given by Bojanus; the third apparently corresponds with an umbilical branch in one of Bojanus' figures, and is probably the margino-costal or epigastric of Hyman. Both of these seem inappropriate names, for it runs within the marginal plates, not within the costal plates, and

does not open anteriorly into the post-cardinal vein or duct of Cuvier. This longitudinal marginal vein is very apt to escape notice, for it runs just at the position at which the carapace is severed from the plastron in opening the tortoise. It seems almost impossible to state, especially in the absence of figures, whether some authors are referring to the common anastomosing branch of the transverse intercostals, or to the longitudinal marginal vein, for both of them connect with the transverse intercostals, the common marginal or epigastric being at a lower level of the carapace. The common descending intercostal or azygous (posterior cardinal) vein runs on either side of the vertebral column as a prominent longitudinal vein. It is connected in front of the pelvic region by a vessel descending (Pl. 28, fig. 1) to the kidney—the anterior renal portal vein. The common descending intercostal or azygous vein is continuous anteriorly with a vein from the other side of the body, which is a branch of the jugular vein of Bojanus (Pl. 27, fig. 3). Posteriorly in the pelvic region it is continued after giving off the anterior renal portals into the common posterior or recurrent intercostal vein to dorsal pelvic muscles. The right and left common descending intercostal or azygous veins are connected with one another at intervals by transverse veins running across the middle line. Each of the common intercostal veins is joined by five lateral or transverse intercostals, running between the costal plates, and by a similar number of short costal veins (vertebral veins of Bojanus) within the costal plates. The transverse intercostals run within the curve of the carapace to within an inch or so of the lower margin, and are there connected within one another by a curved longitudinal vessel, the common anastomosing branch of the transverse intercostals.

Running parallel with the latter, but at a lower level and more lateral, is the common longitudinal marginal vein or epigastric. This is connected at intervals with the common anastomosing branch of the transverse intercostals, but the anterior and posterior transverse intercostals have other connections. The anterior transverse intercostal is connected with the subclavian through a cervical branch of the external jugular (Pl. 27, fig. 3), with a pectoral branch of the anterior abdominal, with the longitudinal marginal or epigastric, and as usual with the azygous. Near the posterior intercostal, the epigastric is connected around the curve between carapace and plastron with a lateral superficial pelvic branch, so that it is placed in communication with the anterior abdominal, and also with the common iliac vein. Anteriorly, the epigastric is connected with the anterior abdominals, and with the veins already mentioned in connection with the anterior transverse intercostal.

In order to complete the circuit of the veins one has to compare the figure given of the veins of the carapace (Pl. 28, fig. 1) with those of the anterior abdominal, renal portals and cervical veins (Pl. 27, fig. 1; Pl. 29, fig. 1; Pl. 27, fig. 3).

The Reno-Reproductive Veins and Posterior Vena Cava (Pl. 28, fig. 3).

The posterior vena cava ("spermatic" of Bojanus) is a very large vein which does not run medianly, but markedly on the right side. Posteriorly it receives renal veins from the kidneys and genital veins from the gonads. The branches from the left gonad and kidney form, more especially in the mature female, an extremely delicate and intricate plexus of vessels which open into the posterior vena cava opposite the entrance of much shorter branches from the right gonad and right kidney. The posterior vena cava then passes in an antero-ventral direction relative to the lungs into the more lateral part of the right lobe of the liver towards its dorsal surface. Anterior to this, the posterior vena cava is again seen as a very large vein, which after receiving several hepatic veins enters the sinus venosus.

Pulmonary Veins.

A right and left pulmonary vein passes from the lung of the respective sides to unite and form the common pulmonary vein which enters the left auricle.

The Hepatic Portal System (Pl. 26, fig. 3).

This system consists of three main parts:—

Firstly, the vessels which pass into a large transverse vein—the main portal—on the dorsal surface of the liver. It receives the anterior abdominal veins from the posterior part of the body, and the latter veins receive branches anteriorly from the liver and pectoral muscles and from the fore-limb and carapace, as already noted.

Secondly, a number of portal veins from the various parts of the alimentary canal which also open into the main transverse portal vein. The more important of these veins are the gastric, duodenal, pancreatic, cystic, splenic, and mesenteric.

Thirdly, the blood conveyed to the liver by the portal vessels mentioned above is carried from it to the sinus venosus mainly by the hepatic vessels; some vessels also pass into the anterior part of the posterior vena cava; the latter before entering the liver lies closely adjacent to the right anterior abdominal.

Anterior Systemic Veins (Pl. 27, figs. 2, 3, 4).

The right and left anterior venae cavae open into a fairly large sinus venosus which is situated slightly asymmetrically. The dissection of the branches of the anterior vena cava is an intricate one, and apparently there has been some confusion by different workers, more especially regarding the jugular vein. It should be clearly noted that there are three, not only two, main veins running along each side of the neck, namely, the œsophageal (Bojanus), the common

vertebral, and the jugular (Bojanus). Pl. 27, fig. 3, shows the branches of the right anterior vena cava as dissected from the side, namely, (*a*) the thyroideal, and (*b*) the scapular; then follow (*c*) the œsophageal (of Bojanus, the internal jugular of Hyman), which comes from the median line of the neck and receives a number of small branches; and (*d*) the subclavian, the largest branch of the anterior vena cava, lying dorsally and laterally, and receiving, firstly, two main branches—(1) the common vertebral (of Bojanus, the external jugular of Hyman), from the brain and face; and (2) the brachial from the fore-limb. The main subclavian receives further dorsally a large vessel—the external jugular (of Bojanus), which receives anteriorly several cervicals from the head and neck, and slightly posteriorly a large vein coming from the dorsal surface; the latter is formed of two vessels already mentioned in connection with the veins of the carapace, namely, one connected with the anterior transverse intercostal, and the other in connection with the common descending intercostal or azygous. Pl. 27, fig. 4, shows parts of these two veins as dissected from the ventral surface, and Pl. 28, fig. 1, as seen incompletely from the dorsal surface of the carapace.

It should also be noted that the branches of the right and left common descending intercostals cross over anteriorly on the dorsal surface, and after the crossing proceed ventrally to connect with the branches of the external jugular already mentioned. There should also be mentioned a small vessel passing into the brachial at a more ventral position, which receives blood from the neck region by passing into connection with the last cervical vein. These component veins of the anterior vena cava agree with the figures given by Bojanus, the differences being only those of nomenclature; but there are discrepancies in some points from the descriptions given by Hyman.

It is interesting to compare the venous system of Testudo with that of *Salamandra maculosa* (see Wiedersheim).

Arterial System.—Anterior Arteries.

The three main anterior arteries, the right aortic arch with the trunk of the innominates as a ventral branch, the left aortic arch, and the common pulmonary, have already been noted from the ventral surface (Pls. 24 and 33). Fig. 2, Pl. 31, shows the innominate, the subclavian branch of the innominate with the carotid and œsophageal branches, the right aorta, and the pulmonary artery, &c., from the dorsal surface and right side, the auricles having been turned upwards towards the left.

The innominate and its branches are not quite similarly placed to those of Emys. The innominate divides into two, and this division forms an anterior V, between the limbs of which lies the thyroid gland. It cannot be well observed in a ventral view (fig. 1, Pl. 31, and Pl. 33) that the innominate is an offshoot from the ventral surface of the right aorta, but a dissection from the dorsal surface makes this point obvious.

There is apparently some lack of uniformity as to what is understood by the term innominate artery in vertebrate animals. The author here uses the term in the manner employed by T. Jeffery Parker, when, in describing the Zootomy of the Pigeon, he writes: "The arch of the aorta is situated immediately external to the right innominate artery, of which it has the appearance of being a branch: the aorta is, however, the principal artery arising from the left ventricle, and the innominates are branches given off immediately after its origin, and, owing to the immense size of the pectoral muscles which they supply, exceeding the remainder of the main trunk in calibre."

It is difficult to show the relationship between the right aortic arch and the innominates in a line diagram, namely, that the innominates are very large branches of the right aortic arch, and this relationship is not expressed in O'Donoghue's "diagram of the arterial arches in *Testudo graeca.*" The very useful generalised diagram of the arterial system of a reptile by Kerr does not quite represent the relationship in this case as regards the lettering. The anterior arteries are, on the other hand, well illustrated diagrammatically in Thomson's figure (after Nuhn), by Goodrich, and in Gegenbaur's figure of the anterior arteries of Chelydra. Hyman notes that the innominates branch off from the right aortic arch. The figure in the present work (Pl. 31, fig. 1) has been criticised by two of my former colleagues, but I subsequently compared this figure with the dissection, and found it to be mainly correct; the artist apparently saw the arrangement of the vessels more clearly than did the critics. A mistake might also be made by examining an injected specimen of *Emys nigricans*, used at Manchester, and falsely assuming that the arrangement was necessarily the same. In the injected specimen of Emys referred to, the fluid appears to have been forced, and to have produced unnatural, distorted results. This specimen of Emys was drawn, but the figure has not been reproduced, as I held it to be misleading. It may be mentioned in this connection that the injections figured in my work were made by a slow, steady flow from a position some height above the specimens.

The subclavian artery (Pl. 31, fig. 1) is continued as the main trunk from the division of the common innominate, but before it becomes the subclavian proper the innominate gives off ventrally the thyroideal to the thyroid gland, and a common carotid dorsally, with a small œsophageal originating near its base. The œsophageal (ventral cervical of Hyman) runs parallel with the common carotid, lies internal to it, and gives off several small branches to the œsophagus, trachea, &c.

The common carotid (Pl. 31, figs. 1, 5; Pl. 37, fig. 1) runs on each side of the neck to the head, giving off branches to the spinal cord, and anteriorly gives off a lingual (internally) and several other branches, including the external and internal carotid, the latter to the brain. A spinal branch of the external carotid anastomoses with an artery, to be mentioned later—the common vertebral.

The subclavian artery (Pl. 31, fig. 4) proceeds laterally and ventrally from the heart towards the great pectoral muscles, and at this part of its course has been termed the descending axillary.

About the middle of the length of the mass of pectoral muscles (taken in a dorso-ventral direction) three arteries are given off from the descending axillary (Pl. 31, fig. 3)—an anterior, termed the internal circumflex humeral; a median, the external circumflex humeral; and a posterior, the thoracic artery. These three arteries originate fairly near one another. The thoracic passes along the posterior surface of the pectoral muscles, and is partly embedded in their substance. It pursues an intricate course, but finally reaches the latero-ventral surface of the carapace, where it breaks up into a number of minute vessels, which pass into connection with the common marginal (or epigastric) artery running longitudinally within the most lateral part of the carapace. The external circumflex humeral also passes through the pectoral muscles, and terminates laterally on those, except for a few branches which anastomose with the artery anterior to it, the internal circumflex humeral. There is sometimes a variation in connection with the external circumflex humeral in the form of a very intricate network of its branches. The internal circumflex humeral, after passing on or through the pectoral muscles, breaks up into many minute branches, which, like the branches of the thoracic, unite with the branches of the common marginal artery. It will be seen later that the common marginal artery places the anterior and posterior parts of the carapace in vascular connection at its most lateral part.

After giving off the three vessels mentioned, the main stem of the subclavian pursues its course in a dorsal and lateral direction, and is now termed the ascending axillary. The ascending axillary gives off three main and two smaller arteries. Of these three main arteries the brachial is the most easily traced; it winds round and passes to the fore-limb, to which it sends off a smaller branch; another branch, the dorsal branch of the brachial, follows, passes dorsally and then ventrally again, to connect with the artery running longitudinally within the curve of the carapace, the common anastomosing branch of the transverse intercostals—the "internal mammary" of Bojanus. The latter artery runs parallel with the common marginal (epigastric of Bojanus), but at a more dorsal part of the carapace.

The second large branch of the subclavian passes dorsally towards the median line of the carapace to connect with the vessel termed by Bojanus the common descending intercostal situated longitudinally and dorsally. An interesting variation occurred in a specimen dissected by Miss Ruth Charlesworth in May, 1928, in which this vessel passed to the dorsal aorta at its formation from the right and left systemics. This second large branch of the subclavian has another branch which connects with the common anastomosing branch of the transverse intercostals. According to Bojanus this artery has also a connection with the genital arteries, and this is supported by some of my dissections.

The third branch of the subclavian from the ascending axillary arises almost opposite the brachial, and passes anteriorly along the neck as the common vertebral of Bojanus, the dorsal cervical of Hymen. It runs to some extent parallel with the common carotid artery, but must not be confused with the

œsophageal lying more ventrally; it anastomoses with a cervical branch of the external carotid anteriorly.

Two smaller arteries are given off near the origin of the last—the scapulars. At the anterior end the common descending intercostal is joined by a small last cervical branch.

These arteries may be traced on the other side of the body from the dorsal surface, in a ventral direction towards the heart. Fig. 2, Pl. 29, represents their course in a general diagrammatic manner. Commencing with the common descending intercostal, an artery passes ventrally, and then divides into two, one branch leading to two anterior intercostals and so to the common anastomosing branch of the transverse intercostals; the other gives off a last cervical, then a brachial, common vertebral, and scapulars. Further in the lateral and ventral direction, as the descending axillary, the subclavian goes off the circumflex humerals and the thoracic, two of which connect with the common longitudinal marginal or epigastric. The subclavian then passes to the innominate, before reaching which it gives off, sometimes at least, a small pectoral. An anastomosis between the brachial artery and the ascending axillary depicted in Pl. 31, fig. 4, may also be mentioned.

The description of these vessels by Hyman does not appear to be accurate, and if this author had seen the classic memoir of Bojanus on the Fresh Water Tortoise Emys she would not have been contented with some points in her own description.

The tracing of the subclavian arteries is difficult owing to the shape of the body of the tortoise, and the great development of large pectoral muscles. The branches of the subclavians have such a tortuous course, passing ventrally, dorsally, and laterally, in such an intricate manner, that, although the main vessels may be made out in a fresh specimen, their ultimate ramifications can only be determined in injected specimens.

The right aortic arch (Pl. 28, fig. 1) is, as already mentioned, concealed from view ventrally at its origin by the large brachiocephalic or common innominate artery which it gives off immediately on leaving the heart. The right aortic arch (Pl. 36, fig. 1) curves dorsally and posteriorly, and during its course may give rise to one or two cardiac arteries to the pericardial region and œsophagus (cardiac of Bojanus). These are not to be confused with the œsophageal which arise as branches from the subclavian artery. They appear to vary in the extent of their development. The left aortic arch, which arises independently of the right arch, curves dorsally and then posteriorly, and unites with the right aortic arch by a narrowed vessel (“*ramus anastomoticus*”) to form the dorsal aorta. From the left aorta, close to its junction with the right, two arteries are given off, each with several branches. These arteries are a large vessel which passes laterally and, after giving origin to a small left cardiac artery to the pericardium and œsophagus, divides into two branches, one passing anteriorly and the other posteriorly. The anterior branch, the gastro-epiploica, runs along the surface of the stomach; the posterior branch, the coeliac of Bojanus, runs in the mesentery (mesogaster) near the stomach, and sends

branches to the pylorus, duodenum, pancreas, liver, and gall bladder (pyloro-pancreatic and hepato-duodenal arteries). The second large artery from the left aorta is concealed at its origin when viewed from the ventral surface by the right aorta and the dorsal aorta; but, when the latter are lifted, a large main vessel is exposed which is apparently double very near its origin, and in some cases there are originally, apparently, two vessels. The branches originating from the main artery are the following:—(*a*) spleno-duodenal, (*b*) anterior mesenteric, with coecal, duodenal, and ileo-coecal (Bojanus), the latter on the looped part of the small intestine, (*c*) the posterior mesenteric to the colon and rectum (art. colica of Bojanus).

In the injected specimen of *Testudo ibera* from which Pl. 35 was drawn, the foregoing branches originated from the left aorta just at its junction with the right to form the dorsal aorta, as is also the case in some other specimens; but this is a feature which apparently varies in different genera, as for example in *Emys nigricans*, in which they arise some distance previous to the formation of the dorsal aorta.

The Pulmonary Arteries (*Pl. 31, figs. 1 and 2; Pl. 37, fig. 1*).

Reverting to the origin of the anterior arteries, the common pulmonary artery proceeds from the right side of the ventricle, and at first runs on the left of the left aortic arch accompanied by a vestige of connective tissue which passes between these two vessels, namely, the ductus arteriosus or ductus Botalli. The common pulmonary then divides into the right and left pulmonary arteries.

The dorsal aorta runs in the medio-dorsal line, and soon after its formation gives off several paired and unpaired arteries which proceed dorsally towards the carapace and peritoneum underlying it—the parietals. The dorsal aorta (Pl. 35) then gives off adrenal, renals, and reno-genital arteries; the latter are not always uniformly developed on both sides. The renal and reno-genital arteries appear to vary in individual specimens according to the age, sex, or degree of sexual maturity. In females in which the eggs are ready to be extruded, the genitals are very large, and their complicated branches are replete with blood. After giving origin to these branches, the dorsal aorta firstly gives rise to a common iliac on each side. These two do not, however, in all cases originate exactly opposite one another. The common iliac has, firstly, a branch which passes dorsally, and which probably corresponds with the recurrent intercostal of Bojanus as it passes to the common descending intercostal and posteriorly to the superior coccygeal; secondly, a branch which corresponds in its place of origin with the recurrent internal mammary of Bojanus—the artery which I term the common anastomosing branch of the transverse intercostals. I am certain that an artery corresponding in position to the internal mammary of Bojanus is present, but a connection between the more anterior part of this and the vessel just described as coming off from the common iliac has been seen neither by myself nor by three other workers who assisted me at this point. The so-called recurrent internal mammary appears rather to pass to abdominal

muscles of the pelvic region and to the bladder. This artery passes ventrally as compared with the previous recurrent intercostal, and I therefore term it the ventral branch of the common iliac.

The common iliac then divides into a posterior branch to the leg (crural) and an anterior branch which passes laterally and anteriorly as the common marginal or epigastric artery—the latter artery is connected at its anterior end with two branches of the subclavian, the internal circumflex humeral and the thoracic, and indirectly with the external circumflex humeral artery.

Returning to the median part of the common iliac arteries as they arise from the bifurcation of the dorsal aorta, there is only a very short median part (sometimes practically none) from which the following arteries proceed. The dorsal aorta is continued medianly at a ventral level into the inferior coccygeal or sacral. On each side of the median sacral a vessel passes posteriorly—the hypogastric. This divides into (*a*) the pudic artery, with hæmorrhoidal, pelvic, cloacal, and penial branches, the latter in the male, and (*b*) the sciatic, which after giving off a branch to pelvic masses divides in the leg into gluteal and obturator branches. The superior coccygeal arteries have already been mentioned.

It must be added that I had corroboration of the course of the common descending intercostals, and of the epigastric as described by Bojanus, and of a connection of those vessels anteriorly with the axillary and posteriorly with the iliac, but I failed to find sufficiently definitely a recurrent vessel connecting with the internal mammary of Bojanus, even in an injected female specimen. In some specimens, however, a tortuous vessel passes in that direction. Unfortunately, I find myself unable to agree with the description of the branches of the iliac arteries given by Hyman.

The Arteries underlying the Carapace (*Pl. 28, fig. 1*).

In the ordinary mode of dissection the arteries and veins underlying the carapace tend to get broken and to come away with it, but in this case the horny plates were firstly removed, and the bony plates then dissolved.

A fact which is not clearly brought out by previous workers, but one which I saw definitely in an injected specimen, is that there are the three main pairs of longitudinal arteries running immediately under the carapace. The first of these three pairs of arteries is:—the common descending intercostal or azygous artery which runs longitudinally along with the azygous or common intercostal vein on each side of the mid-dorsal line. Each common descending intercostal artery sends off in a median direction small branches at intervals to a smaller longitudinal artery, the spinal artery, running on either side of the neural ridge or spine. The second longitudinal artery is one which runs internal to the costal plates, and is formed by the confluence laterally of five transverse intercostal arteries originating from the common descending intercostal artery. It corresponds partly to the recurrent mammary of Bojanus, but may be called the common anastomosing branch of the transverse intercostals. The third

longitudinal artery runs along near the junction of the carapace and plastron, beside the corresponding vein. It receives branches from the last-named, and may be termed the common marginal or epigastric artery. It corresponds with the epigastric of Bojanus and the margino-costal of Hyman. These three longitudinal arteries, the common descending intercostal artery, the common anastomosing intercostal artery, and the common marginal, are connected in different ways with anterior and posterior arteries, namely, with branches of the subclavian in front and branches of the common iliac behind.

The connections are as follows:—the common descending intercostal artery communicates anteriorly with a branch of the ascending axillary already mentioned (Fig. 2, Pl. 29); the common anastomosing branch communicates by another branch with the ascending axillary and with the dorsal brachial; the epigastric or common marginal connects with the internal circumflex humeral, the thoracic, and indirectly with the external circumflex humeral. The common descending intercostal artery gives off five transverse intercostal arteries and also short costals alternate to them. The common descending intercostal artery and the common marginal or epigastric are connected posteriorly, as already mentioned, with the common iliac artery.

The longitudinal spinal artery, which is connected at intervals by branches with the common descending intercostal artery, runs forward along the neck and connects with other cervical arteries. Posteriorly the spinal artery is continued along the dorsal surface of the tail. The common anastomosing branch, which is connected at intervals with the common marginal (epigastric), may have a posterior connection with the common iliac, but this certainly does not occur in all specimens. It has, however, certainly an indirect connection with the common iliac through the common marginal (epigastric). Its anterior connection is with the subclavian through the dorsal branch of the brachial and by two other branches of the ascending axillary of the former.

Neither the arteries nor the veins differ so much from those of other vertebrata as might at first sight be supposed. If space permitted, this would be shown, but it may be pointed out, for example, that although there seems a great complexity of the veins in connection with the carapace, this is understandable in view of the absence of muscles between the parietal peritoneum and the skin or skin derivatives. Many of the veins of the carapace take the place of the musculo-cutaneous and other veins of different vertebrata.

The Structure of the Chelonian Heart.

The sinus venosus, which is situated dorsally and to the right of the median line, is fairly well developed; it receives blood from the anterior venae cavae and the posterior vena cava, which then passes through the sinu-auricular aperture into the right auricle. The sinu-auricular aperture situated at the right posterior side of the right auricle is provided with two valves which are continued as flaps for a short distance along the wall of the auricle. The right auricle, receiving as it does all the venous blood from the body generally, is larger and thicker walled than the left auricle, from which it is separated by

the inter-auricular septum or septum auriculorum. The left auricle receives blood from the two pulmonary veins through a small single aperture which is situated on its median dorsal surface, and is not provided with well-marked valves.

The ventricle has thick walls, consisting of muscles and trabeculae, which form a loose spongy tissue; muscular bands and connective tissue—the gubernaculum cordis — extend from the apex of the ventricle to the wall of the pericardium. The cavity of the ventricle is partially divided into two by a muscular septum which is partly marked out superficially by the external interventricular sulcus; this septum is essentially a ventral one which extends from the left ventral wall towards the right in an oblique dorsal direction into the ventricular cavity. It thus tends to divide the ventricular cavity into two, namely, a left dorso-lateral chamber and a right ventro-lateral chamber. It is therefore termed the oblique or interventricular septum. It is, to some extent, continuous with the inter-auricular septum which divides the atrium into left and right auricles, but, whereas in the case of the latter the arterialised and venous blood are completely separated from one another, in the former there cannot be such a complete separation, as the interventricular septum does not reach the dorsal surface. (Goodrich, Journal of Anatomy, Pt. IV, July, 1919, Fig. LIII; and Proc. Roy. Soc., B, Vol. 89, 1916, Fig. 4, C, p. 273.)

In the Chelonia, as in other Reptilia, the auriculo-ventricular aperture is divided into two by the inter-auricular septum, and each of the openings so formed is provided with two valves, namely, a left auriculo-ventricular marginal and a left septal (medial) auriculo-ventricular valve, a right auriculo-ventricular marginal, and a right auriculo-ventricular septal valve. (Goodrich, Fig. 1, July, 1919.)

The smaller right or ventro-lateral chamber of the ventricle—the cavum pulmonare—from which the pulmonary artery proceeds "is continued up on the right of the free edge of the septum" into the more dorsally situated part of the ventricular cavity, the cavum venosum, from which the left systemic originates. The left, or dorsal-lateral, chamber is the cavum arteriosum, from which the right systemic and the innominates originate. On the right side of the base of the interventricular septum is the ostium of the pulmonary artery, and the septum separates the pulmonary opening from the more dorsally situated aperture of the right systemic (carotico-systemic).

The rough figures of transverse sections of the Chelonian heart by Goodrich ("Note on the Reptilian Heart") show the positions of the auriculo-ventricular openings and auriculo-ventricular valves. The auriculo-ventricular apertures are seen as slits right and left of the median line of the ventricle. They are completely separated from one another by a left septal (medial) auriculo-ventricular valve and a right septal auriculo-ventricular valve, and the left and right apertures are also guarded externally and laterally by the left and right auriculo-ventricular or marginal valves. It is obvious that the left auriculo-ventricular aperture is the inlet for the oxygenated blood which passes into the left auricle from the pulmonary vein. The right auriculo-ventricular

aperture, on the other hand, is that for the inlet of venous blood from the body through the sinus venosus into the right auricle. With the help of the medial septal auriculo-ventricular valves, the bulk of the venous blood passes ventrally at auricular systole round the free edge of the septum into the cavum pulmonale, while the bulk of the arterial blood passes across to the right systemic arch. In the Chelonian heart the left systemic arch thus receives most of its blood from the cavum pulmonare and the right arch from the cavum arteriosum.

"It will be gathered . . . . that in the anterior region of the ventricle of these Reptiles there are two streams of blood crossing each other almost at right angles. The more anterior arterial stream passes from the left region (cavum arteriosum) across to the right arch, and the more posterior stream passes downwards from the right region (cavum venosum) to the cavum pulmonale. Before reaching the base of the various arches the blood passes towards the apex of the heart; and if we follow backwards the three cavities mentioned above (cavum arteriosum, c. venosum, and c. pulmonare) we find that the cavum arteriosum forms in all the three groups (Chelonia, Lacertilia, and Ophidia) the incipient left, while the cavum venosum and c. pulmonale belong to the incipient right ventricle." (Summary, Goodrich.)

"There is in the ventricle of all living Reptilia a muscular septum attached to the ventral wall and passing forwards between the left auriculo-ventricular opening and the ostium of the pulmonary artery. Dorsally and to the left of this septum is the cavum arteriosum, while on the right the dorsal cavum venosum passes ventrally round the free edge of the septum to the cavum pulmonale. Muscular strands from the base of the septum to the dorsal wall of the ventricle separate incipient left from incipient right chambers. In the Crocodilia these strands form a wall, which together with the septum unite with the endocardial cushion of the inter-auricular septum, and complete the division of the cavity into a left ventricle, corresponding to the cavum arteriosum, and a right ventricle, corresponding to the cavum venosum and the cavum pulmonale. The left ventricle leads to the right aortic arch, and the right ventricle to the pulmonary artery and the left aortic arch. Whereas in the Chelonia, as in the Crocodilia, the left arch receives most of its blood from the cavum pulmonale; in the Lacertilia and Ophidia it opens more dorsally so as to receive arterial blood as well." (Goodrich.)

As compared with the Amphibia, a great step in the evolution of a separation of the blood stream has taken place in the disappearance of the conus arteriosus, and the breaking up of the truncus into the three canals, namely the right and left aortic arches and the pulmonary, the right arch arising from the left dorso-lateral side of the interventricular septum, the left arch from the right dorsal side, and the common pulmonary from the right ventro-lateral side of the septum.

There is no longer a ductus Cuvieri but a ductus Botalli is present. It is obvious that the carotids and the subclavians receive oxygenated blood, but that, as the coeliac and mesenteric arteries originate from the left systemic, parts of the alimentary canal supplied by the branches of those will mainly receive

de-oxygenated blood. The posterior anastomosing branch between the left aorta and the right aorta, which unite to form the dorsal aorta, is a narrow vessel, and it is more than probable that most of the venous blood passes to coeliac and mesenteric branches rather than to the dorsal aorta, therefore the blood of the dorsal aorta will be almost completely arterialised blood.

The author is indebted to the papers by Goodrich for this statement. He regrets he is unable to agree with some points in those by O'Donoghue.

The Lymphatic System.

Joh. Müller first called attention to the occurrence of lymph hearts in the Chelonia when he observed them in a fresh terrestrial tortoise on removing the posterior end of the carapace at a position slightly behind the dorsal extremity of the ilium. He also observed their pulsations in two living specimens of the pond tortoise, *Emys europae*. Subsequently he investigated them in a very large living specimen of the turtle, *Chelone midas*. The exact position of the two lymph hearts may be determined by taking the medial longitudinal line on the most posterior shield at the carapace and dividing it into three equal parts; when lines are drawn at right angles to the two points of equal distance on this line, the second transverse line, which separates the second and third parts, indicates the position of the two lymph hearts; they are situated, namely, in the direction indicated just beneath the bony plate, being covered over otherwise only by connective tissue and fat. This line only indicates the distance of the lymph hearts from the posterior end of the carapace. Their position may be more exactly indicated by stating that if one divides the specified transverse line of the posterior median shield into three equal parts, the dividing points would once again indicate the position of the hearts and their distance from one another. They can, therefore, be exposed by cutting out and carefully detaching a square containing the points indicated from the posterior part of the carapace. The lymph hearts are situated, one on each side, adjacent to and posterior to the dorsal extremity of the ilium.

The lymph heart was seen to receive at its external posterior part a series of large lymph vessels, which conducted lymph from the hind limb, and, posteriorly also, vessels which collected lymph from the postero-ventral surface of the abdomen. The hearts appeared to contract powerfully and regularly three or four times per minute, and the contractions were sometimes, but not invariably, simultaneous. When one of the lymph hearts was cut, the lymph was seen to be poured out periodically at each contraction.

In the Chelonia, in general, lymph spaces of variable size occur irregularly distributed at almost any part of the body, and there are also canals or vascular channels which follow the direction of the longitudinal axis of the body in the dorso-lumbar and caudal regions, and which, as a rule, pass in the same direction as the great arterial trunks.

The author desired further opportunity of investigating certain puzzling

parts, which appeared as relatively large swellings, apparently of the blood vessels, more especially in injected specimens.

For further details regarding the lymphatic system, reference should be made to the works of Müller, Hoffmann, and Fritsch.

The Ductless Glands.—The Thymus.

The present writer is unable to make any very definite statements regarding the occurrence of the thymus in *Testudo ibera* and *Testudo graeca*; Leydig did not observe the thymus in the latter species, but the apparent absence may have been due to the relative degree of maturity of the specimens which were dissected, as there is no doubt that the thymus, as a general rule, varies in size at different ages, and seemingly tends to disappear when development is completed. On the other hand, Fritsch mentioned the occurrence of the thymus in an adult *Testudo elephantina*. Hoffmann found no trace of the thymus in *Emys europaea*, and in the latter species Bojanus figures the thyroid under the term thymus.

During a dissection of "*Chelonia*" *caretta* (*Thalassochelys corticata*), Ecker found the thymus lying between the carotid and the subclavian arteries, and described it as an extremely vascular greyish black organ, with a structure similar to that of the thymus of birds.

Stannius stated that in the newly hatched young of *Chelone midas* the thymus, similarly as in young birds, extends along the entire length of the neck from the lower jaw anteriorly to the commencement of the thorax posteriorly. Owen stated that in young specimens of the genus Chelone, the thymus occurs as an oblong yellowish-white body, situated on each side between the carotid and the axillary arteries, and that it apparently degenerated in older specimens. Jones stated that he had observed a small organ in young tortoises which resembled fat in external appearance, but which on microscopic examination presented the characteristic appearance of the thymus.

Among the more recent investigators of Vertebrate Anatomy, Hyman writes, "the thymus gland in the turtle is a yellowish mass lateral to the ventral cervical artery, and receiving branches from it."

Thyroid Gland.

The thyroid gland is a flattened, irregularly rounded body, of considerable size, yellowish brown or reddish in colour, which is situated anterior to the heart, between the bifurcation of the common innominate artery (Pl. 37, fig. 1). This was, as already mentioned, termed the thymus by Bojanus. Leydig described the structure of this gland in *Testudo graeca*, and Hoffmann of that in *Emys europaea*, in which it is apparently similar. It would be interesting to know more about the functioning of this gland in this creature of long life and slow metabolism.

Adrenal Bodies.

The adrenal bodies are situated along part of the internal surface of each kidney (Pl. 37, fig. 2), from which they are distinguished by a different texture and colour. These were first described by Morgagni and Bojanus as long glandular bodies, occurring on the internal margins of the kidneys in European tortoises. They were figured by Bojanus under the term *Ren succenturiatus*, and the term adrenal bodies is most frequently synonymous with "nebennieren."

Nagel confirmed the occurrence of adrenal bodies or "nebennieren" in *Emys europaea*, and described them as "two yellowish red bodies"; various authors have noted their presence in other Reptilia, such as in snakes and lizards, but their occurrence is not universal.

In their description of the Red-Bellied Slider Terrapin (*Pseudemys rugosa*), Martin and Moale wrote, "Note the bright yellow adrenal body lying along the mesial border of the kidney." Hoffmann described the "nebennieren" of *Emys europaea* as consisting of two parts, namely (*a*) of variously shaped masses of yellow cells, and (*b*) of a tubular part. The reader is referred to the more detailed description of the "Nebennieren" or adrenal bodies given by Hoffmann in the chapter on Blutgefässdrusen-Milz-Nebennieren. Thyreoidea. Thymus.[1] Hyman apparently does not refer to the adrenal bodies in the description of the "Urogenital System of the Turtle."[2]

The spleen has been previously mentioned in connection with the description of the alimentary canal; it is a rounded, reddish body situated in the mesentery to which the large intestine is attached, a little distance beyond the coecum.

Section 8.—Buccal Cavity and Respiratory Organs. (*Pl. 20, figs. 3–8; Pl. 32, fig. 6.*)

The Tongue—Lingual Muscles—Apertures in the Buccal Cavity—Glottis and other respiratory parts.

The tongue occurs in the usual position on the floor of the buccal cavity. The bones which bound the mouth cavity laterally, namely, the premaxillae, maxillae, and dentaries, are covered by the horny plates already mentioned, which fit very accurately over these bones of the upper and lower jaw. These horny plates are epidermic in origin and have sharp cutting edges, sometimes with notches; the plates are very easily detached from the remainder of the skull during maceration, and are very liable to become lost. True teeth do not occur.

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[1] Bronn's Klassen und Ordnungen des Thier-Reichs, Hoffmann, C. K. Sechster Band, III Abtheilung Reptilien I Schildkroten.

[2] Hyman, Libbie Henrietta. A Laboratory Manual for Comparative Vertebrate Anatomy.

The Tongue.

The tongue of Chelonia has less freedom of movement than that of the other Reptilia; its structure varies in the different sections of the order. Its surface is beset by numerous long, soft papillae, which Leydig first described in *Testudo graeca.* Hoffmann and Oppel subsequently reinvestigated their structure. The primary papillae are provided with knob-like processes or secondary papillae, and the surfaces of both are covered with stratified epithelia. Blood vessels and nerves run within the papillae, and smaller nerve branches radiate out to taste buds occurring on the epithelia of the papillae. The taste buds consist of tall, cylindrical, sustentacular cells and taste cells proper with forking processes. Lingual glands open either at the bases of, or near the apices of, the papillae; there are large salivary glands beneath the tongue in Testudo termed sub-lingual (Bojanus and Hoffmann). These are sacculated glands which open by ducts on the surface.

Oppel states "that glands are present in the Chelonia (Testudo) on both sides of the tongue, which are comparable with the glands of the lower jaw of higher animals." The mass of the tongue consists of muscles, connective tissue bundles, and elastic fibres, and its surface is a stratified squamous epithelium.

In view of the fact that good descriptions and figures of the histology of the tongue are given by Bojanus, Hoffmann, and Oppel, it appears unnecessary to repeat them in this monograph.

Lingual Muscles.

There are two principal lingual muscles, the *musculus maxillo-glossus* and the *musculus cerato-glossus* or *musculus hyo-glossus.*

The *Musculus maxillo-glossus,* syn. *Genio-glossus,* Bojanus, Owen, Stannius, Cuvier, originates from the medial part of the inner surface of the lower jaw and is inserted into the hyoid body and the os entoglossum.

The *Musculus cerato-glossus,* syn. *Hyoglossus,* Bojanus, Owen, Cuvier, Stannius, originates from the second pair of cornua, and is inserted into the body of the hyoid and the os entoglossum.

Apertures in the Buccal Cavity. (*Pl. 32, fig. 6.*)

In the anterior portion of the cavity posterior to the horny epidermic plate covering the upper jaw there are diverging folds of mucous membrane between which are seen the elongated openings of the posterior or internal nares, with the posterior edge of the septum narium between them. It should be noted that the eyeballs do not cause projections on the roof of the mouth as in the frog, but are completely separated from it by a hard palate. On the floor of the mouth, at the base of the tongue, there is a considerable elevation in which is a longitudinal slit, the glottis. The opening of the Eustachian tube, which communicates with the cavity of the middle ear, is situated one on each side of the roof of the pharynx posterior to the muscles which run between the skull

and the lower jaw. The pharynx or posterior continuation of the oral or mouth cavity narrows and passes into the oesophagus.

The Respiratory System.

The position of the glottis has already been noted. The trachea is exposed by cutting through the skin in the mid-ventral line of the neck and throat, and then separating the muscles in the same position. Anteriorly the trachea is expanded on the dorsal surface of the body of the hyoid into the larynx, on the lateral walls of which are the arytenoid cartilages, one on each side, and these support the two triangular flaps which enclose the glottis. The cricoid cartilage is situated posterior to the glottis; it is much wider on the ventral than on the dorsal side.

The muscles of the larynx are the *M. constrictor larygngis*, syns. *Constrictor glottidis* (Bojanus), *Constrictor laryngis* (Hense), and the *Musculus dilatator laryngis, Dilatator laryngis* (Hense).

The less expanded part of the trachea follows the larynx; it is situated ventral to or on one side of the oesophagus. The course of the trachea in the genus Testudo is comparatively short, as it divides almost immediately behind the hyoid into the two bronchi, but in most other genera it has a longer course previous to its bifurcation. The epithelium of the trachea and bronchi consists of tall ciliated cells and of goblet cells; the corium of the mucous membrane is very thin, but it contains numerous blood-vessels and large lymphoid spaces. On account of the mucous present in the cavity it is necessary during the dissection to wipe it away with a little bit of sponge held by a small pair of forceps. The bronchus of each side is accompanied by a pulmonary artery and vein. The lungs, which are very extensive, are exposed from the ventral surface by raising the lobes of the liver and the stomach. From the dorsal surface they appear as large spongy organs, one on each side immediately under the carapace, and extending into contact with the greater part of the length and breadth of the latter.

It is important to note that the lungs are mostly in contact with the inner surface of the carapace, and that the parietal peritoneum passes over their ventral surfaces, and thus that the lungs are outside this membrane. Such a relationship between the lungs and the peritoneum is described as retro-peritoneal (see coelom). While the above holds true for the greater part of the length of the lungs, it does not prevail in the posterior part, as here the lung projects into the pleuroperitoneal cavity and is invested by the peritoneum.

Oppel has given a diagram of the compound lobulated lung of *Testudo graeca*. The lung is no longer a single lobular one, as in the frog, but consists of 8, 10, or 12 lobules situated in proximity. The bronchus is continued right down along the internal margin of the lung, and there are a series of circular apertures, homologous with bronchioles, leading into the lobules. Fibrous connective tissue cords pass from the bronchus into each lobule and divide it up; each lobule is composed of smaller or minor lobules. Afferent arterioles and

venules are seen. The bronchi and the apertures are covered with ciliated epithelium. Oppel has also given a figure (after Schulze) of the epithelium of the internal alveolar wall of *Testudo graeca,* which consists of flat polygonal cells and cells with conical projections which enter into close association with the capillary network on the surface of the lung.

During respiration air passes through the following parts in the order in which they are named: anterior nares, buccal cavity, pharyngeal cavity, glottis, larynx, tracheae, bronchi, and lungs.

The characteristic feature of the mode of respiration has already been noted.

Mode of Respiration.

The breathing, like most processes in the Chelonia, is slow. The slow rate of breathing is a necessary corollary from the occurrence of a fixed carapace holding the lungs relatively fast; there cannot be the same freedom of lung action that is associated with bird and mammal. Under the shelter of the carapace the lungs are filled and emptied, partly by the alternate extension and retraction of the head and neck, and partly through the action of the hyoid apparatus, by which, when the neck is extended, air is alternately pumped in and released through the glottis.

SECTION 9.—RENO-REPRODUCTIVE SYSTEM. (PL. 36, FIG. 3; PL. 37, FIG. 2; PL. 38; FIGS. 1, 2.)

Female urinogenital organs—Ovaries—Oviducts—Kidneys—Adrenal Bodies—Ureters—Urinogenital Sinus—Urinary Bladder—Cloaca—Clitoris—Male genital organs—Testes—Epididymes—Vasa efferentia—Vasa deferentia—Urinogenital Sinus—Penis—The Cloaca and adjoining parts in Chelonia in general.

The reno-reproductive organs are exposed by removing the greater part of the alimentary canal, with the exception of the posterior part of the rectum which may be left in its natural position. The female genital system consists of a pair of ovaries and a pair of oviducts (Müllerian ducts). The ovaries are orange-red masses situated in the posterior part of the pleuroperitoneal cavity, and usually contain numerous ova of graded sizes. In the fuller mature female the ovaries are very extensive, and tend to conceal the other anterior and the posterior viscera. They are invested by the parietal peritoneum, and are supported by a mesentery, the mesovarium. The oviducts are situated along the lateral and posterior borders of each ovary; they are long, white tubes, suspended by a mesentery, the mesotubarium. At their anterior ends the walls are extended around the ostium or opening into the abdominal cavity. The ostium opens by a wide mouth into the pleuroperitoneal cavity dorsal to the posterior extremity of the lung. Posteriorly, each oviduct passes ventro-lateral relative to the rectum and dorsal to the ischio-pubic bridge to open into the

urinogenital sinus. The kidneys are large, reddish bodies, situated against the posterior end of the pleuroperitoneal membrane in the concavity of the carapace, slightly posterior to the ovaries; their ventral surfaces show marked convolutions. Elongated ureters extend from the kidneys to their openings into the urinogenital sinus at a point slightly latero-posterior to the openings of the oviducts. When the cloaca is laid open along its entire ventral surface, there come into view the urinogenital sinus anteriorly, with the opening of the neck of the urinary bladder, and with the openings of the oviducts and ureters, the aperture of the rectum (anus) situated more dorsally further posteriorly, and a specialised part of the cloacal wall, the clitoris or homologue of the penis.

The urinary bladder is a conspicuously large and wide thick-walled sac, narrowing posteriorly into a neck, which connects with the urinogenital sinus adjacent to and in front of the apertures of the ureters and oviducts, and ventral to the large intestine. It has been repeatedly observed that the urine is retained in the bladder for lengthened periods. The bladder is situated adjacent to the pubic bones, and is connected with the latter by a ventral fold, in a similar manner to that in the Mammalia. When it empties it becomes contracted in a folded manner. It is invested by the pleuroperitoneal membrane; its wall consists of a muscular and a mucous layer, and is also well supplied with blood vessels. There is a complicated system of muscles and elastic fibres in connection with the passage of the neck of the bladder into the urinogenital sinus, or anterior part of the cloaca, which act in connection with the evacuation and distension of the bladder. The opening of the neck of the bladder into the urinogenital sinus has been termed the *ostium vesico-urethra.*

In younger specimens the ovaries are long, oval, paired organs, but in mature specimens they form an irregular sack-like body. A summary of the papers on the structure and development of the ovary and ovarium follicles of the Reptilia is given by Hoffmann; there are apparently numerous points of similarity, more especially in regard to the ovarian follicles, with that of birds. The oviducts serve to conduct the ova to the exterior, and they also secrete the egg membranes and the shells, the latter consisting of fibrous matter and calcareous salts. The abdominal openings or ostia of the oviducts are ciliated, and other parts of the mucous parts of the wall have numerous, minute, racemose glandular canals.

In Chelonia the clitoris lies on the wall of the cloaca in the female in the position at which the penis is situated in the male. The body of the clitoris consisting of connective tissue fibres may either be attached to the wall of the cloaca throughout its entire length, or there may be a much more intimate fusion with the cloacal wall. The degree of development of the clitoris varies in the young and adult. Rathke pointed out that in older embryos and in the young the clitoris was relatively large and the penis small as compared with the size of the body. The structure and histology of the clitoris are generally comparable with those of the penis. When well developed, the structure of the clitoris in *Testudo graeca* is in essential features similar to that of the penis.

The functional kidney of the adult tortoise is a metanephros, but Van

Wijhe and others have noted the occurrence of vestiges of the mesonephros and wolffian duct in a female specimen of *Emys europaea*. In this case the wolffian duct was situated beside the ureter in a similar position to that of the vas deferens in the male, and a number of small transverse tubules represented the mesonephros. The functional kidneys or metanephros are conspicuously large, lobed organs. The lobes form a fairly compact mass; on the ventral surface they present a remarkable convoluted appearance resembling cerebral gyri or convolutions. The kidney, as viewed from the ventral surface, is divided into three regions, two anterior and one posterior, each of which is subdivided into several minor lobes. The surface of the kidney is invested by a pigmented connective tissue membrane, which is prolonged into the lobes of the kidneys; many blood vessels pass through this membrane, and pursue a tortuous course over the surface of the kidneys. Van Wijhe has given an account of the histological structure of the kidneys, in which he describes malpighian capsules, uriniferous tubules, Henle's layer, and the connecting canals leading to the ureter.

The adrenal bodies are more easily seen in the male; they have already been noticed in connection with the ductless glands.

The ureters are not enlarged at their exits from the kidney as they are in the Mammalia; in other words, a pelvic expansion is not formed. In the female the ureter opens into the urinogenital sinus at a point slightly external or latero-posterior to the aperture of the oviduct; in the male the renal and genital openings of each side are situated very close together on a slight swelling, and are so closely adjacent as almost to form one aperture.

The male reno-reproductive organs consist of the kidneys, adrenal bodies, ureters, urinary bladder, urinogenital sinus, testes, epididymes, vasa efferentia, vasa deferentia, and penis. The testes are long, yellow, oval bodies, which are attached by the mesorchium to the ventral surface of the kidneys. The epididymes are long coiled bodies, which are situated laterally and posteriorly to the testes; they are invested by a black pigmented peritoneal membrane, and when the latter is removed, long coiled ducts are exposed which proceed in a distal direction and become continuous with the vas deferens: the latter opens, beside the ureter and near the opening of the neck of the urinary bladder, into the urinogenital sinus, in front of the anterior part of the penis. The opening of the rectum into the cloaca is situated more dorsally. The parts intervening between the testes and the distal end of the vas deferens, as it enters the urinogenital sinus, are very complicated and extremely difficult to follow. At the part where the vasa efferentia leave the testis there is a considerable proportion of mesh-like tissue which is interlinked not only with the lining membrane, but with the interior of the testes. In this mesh-like tissue there are numerous vasa efferentia embedded in connective tissue with a complicated system of muscle fibres; the vasa efferentia have very narrow lumina, and in sections they are distinguished from the remainder of the tissue by the occurrence of spermatozoa. The extremely coiled vas deferens, to which the vasa efferentia proceed, is similarly surrounded by connective tissue and muscle fibres, so that

the two are extremely closely interwoven. For these reasons it is almost impossible to follow the exact course of the vas deferens, more especially as the muscle fibres surrounding it do not always run in the same or in any definite direction, but in a very irregular manner. In sections, however, the irregular distribution of the vas deferens may be distinguished by recognising the occurrence of spermatozoa, with the usual structure.

In Testudo and other Chelonia, as contrasted with Amphibia, the excretory duct is separate from the genital duct in both sexes; but there is in the Chelonia a very intimate connection between the kidneys and the epididymes, and between the vasa efferentia and the ureters, so that it appears impossible to determine exactly in those cases where the one part ends and the other begins except in sections.

Persistent Müllerian Duct in the Male.

In the male, at a place corresponding to that of the anterior end of the oviduct in the female, there is a slight fold of the peritoneum. The posterior end of this peritoneal fold gradually merges into the wall of the vas deferens, and disappears from view not far from the opening of the latter into the urinogenital sinus. The fold extends along the lateral surface of the vas deferens, but it becomes smaller anteriorly until it finally disappears. It is along this peritoneal fold that the Müllerian duct is situated, its anterior end terminating in a small dilatation placed dorsal to the posterior end of the lung, and its posterior running into the urinogenital sinus, near the apertures of the vas deferens and ureter. The duct varies in the extent of its development in different specimens and species, and is sometimes entirely absent, but, when well developed, is to be regarded as the unaborted Müllerian duct of the embryo, and therefore homologous with the oviduct of the female.

The penis is situated on the ventral wall of the cloaca; it is protracted by a paired muscle (*musculus protrahens penis*, Bojanus), which is inserted on the ventral surface of several of the posterior trunk vertebrae, and terminates at its base. The penis appears to originate as elongated lateral projections (corpora cavernosa) of the ventral wall of the cloaca, which gradually come to surround a groove, extending along the dorsal surface throughout the greater part of its length. At the extremity there is a free enlargement—the glans penis. Joh. Müller described the structure of the male copulatory organ of giant tortoises, and Hoffmann and Schmidtgen similarly for the species, *Testudo graeca* and *Emys europaea*. Bojanus had excellent figures and descriptions of the urinogenital organs of the latter species.

Bursae Anales.

Blind sacs or anal bursae open, like the urinary bladder, into the cloacal chamber, in a number of species of Chelonia, but they do not occur in the genus Testudo.

The Cloaca.

The muscles of the cloaca are the *sphincter cloacae* (Bojanus), *sphincter vestibuli* (Budge), and the *dilator cloacae* (Bojanus), *levator vestibuli* (Budge). According to Budge a strong and broad muscle, the *sphincter vestibuli*, surrounds the vestibule and cloaca on either side. It is situated between the carapace and the ischia, and its bony attachments are to the latter, and to the ventral surfaces of the sacrum and coccyx. The other muscle of the cloaca, the *musculus levator cloacae* of Hoffmann, the *dilatator cloacae* of Bojanus, the *levator vestibuli* of Budge, is regarded as analogous with the similarly named muscle in the Mammalia. It appears, however, to be much narrower than in the latter. It originates on the dorsal surface of the pubis, proceeds over one of the adductors of the thigh; it then runs posteriorly over the ischium, crosses the retractor penis muscle, reaches the external wall of the vestibule, exchanges fibres with the sphincter, then gives off other branches to the rectum, and finally passes over to connect with tendons, which are attached to the ischia. This muscle probably acts in connection with the expulsion of the urine, the genital cells, and the faeces.

General.

Peritoneal canals are known to occur in many, if not all, species of Chelonia, including *Testudo graeca*. They are evaginations of the body cavity, the anterior or abdominal apertures of which are situated in a "neck of the peritoneum" close to the sides of the neck of the bladder, and the posterior or cloacal terminations in front of the glans penis in the male, at the commencement of the clitoris in the female. It is disputed whether the canals always communicate with the cloaca in the male (Schmidtgen, Anderson, Gadow). Gadow suggests that the function of the peritoneal canals may be to drain away any excess serous fluid from the abdominal cavity; more especially when the latter is filled with eggs, or when the canal apparently ends blindly in the male, to receive fluid which becomes compressed, and assists erection.

Schmidtgen gives the following account of the structure of the cloaca and related parts in *Testudo graeca* (Taf. 33, figs. 15, 16):—

The rectum passes imperceptibly into the cloaca, a circular sphincter is not present, the diameter of the rectum is the same as that of the cloaca. The wall of the cloaca has longitudinal folds, a slight amount of pigmentation occurs, but only on the last quarter of its length. The opening of the urinogenital sinus occurs as a median slit-like aperture on the ventral surface. When one prolongs this opening anteriorly, during which one cuts through the ventral surface of the rectum, and the dorsal surface of the neck of the bladder (urorectal septum of Möller), one sees the opening of the urinary bladder into the sinus. The urogenital papillae lie laterally and slightly posteriorly to the latter opening, but are deeply hidden by a membranous fold. The genital papillae consist in this case of a quite small swelling on each side. The vas deferens opens

at the apex of, and perforates the papilla, the opening of the ureter is medial and at the base. The vas deferens and ureter run so close together in the wall of the cloaca, that they are difficult to dissect apart. The wall of the urinogenital sinus has large, longitudinal folds, including two specially strongly developed folds on the ventral surface at the point where the sinus enters the cloaca. The seminal groove originates between these two longitudinal folds near their posterior end, and passes to the apex of the penis. The cloaca of the female is similar, except that the opening of the urinogenital sinus is slightly larger than in the male, the urogenital papillae are more prominent, and there is not any pigmentation.

Sinus Urogenitalis.

Schmidtgen defines this sinus as a special hollow chamber into which open the bladder, the ureter, and the genital ducts. The urinogenital sinus has arisen by the growing together of two longitudinal folds which originate lateral to the urogenital papilla (this fused part v. Möller termed the *urorectal septum*). It cannot be regarded simply as a prolongation of the narrow neck of the bladder. The numerous longitudinal folds in the wall of the neck of the bladder do not grade over into the wall of the urinogenital sinus. Transverse sections of the cloaca of a young specimen of *Emys orbicularis* showed the sinus urogenitalis at this early stage as a hollow space in front of the opening of the bladder under the rectum.

The complete growth of the longitudinal folds, from which the urinogenital sinus is formed, does not take place until the post-embryonic stage. In transverse sections such as those mentioned above, the longitudinal folds have not yet grown so completely together to form a true urinogenital sinus. At first the fusion has only taken place as far as the opening of the ureter, the vas deferens still opens directly into the cloaca. At an early stage of *Chelone imbricata,* in which the growth was not completed, both the uteri and ureters still opened into the cloaca.

Schmidtgen has given the following description of the structure of the penis of *Testudo graeca*:—

"The anterior half of the penis is situated on the cloacal wall, the posterior part projects in the cloaca. The root of the penis consists of thick strands of cavernous tissue which extend fairly far anteriorly; they are partially darkly pigmented. The fibrous bodies soon appear in them, and unite near the position where the urinogenital sinus opens into the cloaca. They form a slight S-shape curve shortly before the point where they fuse. The fibrous body is not very broad, but comparatively thick, its margins are slightly curved upwards. It runs, gradually becoming reduced in size, to the external pointed apex of the penis. The fibrous body consists of a very firm external and a looser internal zone, and blood corpuscles are seen to occur in the spaces intervening between the fibrous cords of the latter. The seminal groove commences at the

part where the fibrous bodies unite together, and terminates before the apex on the anterior base of a semi-circular fold of skin which curves over in a posterior direction. A strong rounded ridge is situated around this fold. The cavernous tissue decreases in a gradual manner as the fibrous body appears; it is altogether absent in the medial parts of the penis, but the most posterior part and its ridges again consist of this kind of tissue. A large lacunar blood sinus runs posteriorly, under the mucous tissue, on each side of the seminal groove in the bay-like space which originated by the curving upwards of the margins of the fibrous body. It connects the cavernous tissue of the root of the penis with that of the apex, and is partly filled with blood. The penial artery runs in its wall, and supplies the hollow spaces in the apex with blood. Schmidtgen has given a summary of the work previous to his own on the structure of the penis. His statements are not, however, always exactly accurate. The author would draw special attention to the work of Gadow on the structure of the cloaca and adjoining parts in the Chelonia.

SECTION 10.—THE NERVOUS SYSTEM—THE MUSCULAR SYSTEM.

The Spinal Cord—The Brain—The Origin of the Cranial Nerves—The Distribution of the Cranial Nerves—The Sympathetic Nervous System—The Cervical Nerves—The Brachial Plexus—The Dorso-lumbar Nerves—The Lumbo-sacral Plexus—Reference to the Muscular System.

The Central Nervous System.

The Spinal Cord, as in other Vertebrata, extends as a more or less cylindrical cord from the posterior end of the head to the extremity of the tail. The diameter is not equal throughout its entire length, for it has an anterior, or cervical, and a posterior, or lumbar, enlargement. Between the medulla oblongata and the cervical enlargement, there is a slight decrease in its diameter, and between the cervical and the lumbar enlargement, namely in the dorsal or thoracic region, there is a greater diminution; posterior to the lumbar dilatation of the cord, and extending to the extremity of the tail, there is a continuous reduction in the diameter (caudal region).

Bojanus has given four figures of the entire central system of Emys, as dissected from the dorsal and ventral surfaces (Bojanus Pl. 21, figs. 83 and 84) but except for the facts mentioned above there does not appear to be much point in adding similar figures in the present monograph.

As viewed in section, the spinal cord is sub-elliptical, except in the dorsal region, where it is sub-circular. A ventral fissure is present on its lower surface medianly, which varies in depth at different parts of the cord, thus it apparently decreases in size from the lumbar to the caudal region. The dorsal fissure also varies, being practically absent in the anterior region but partially present in the lumbar region and further posteriorly.

Hoffmann has given figures of sections of the brain and spinal cord of *Testudo græca* (after Stieda) Tafel XXIV, figs. 1–12.

The spinal nerves, with the exception of the first and second, are provided with the usual dorsal and ventral roots, the former have only ventral roots. The dorsal roots are enlarged as usual into the spinal ganglia. The spinal nerves vary in size and in the distance between them at different regions of the spinal cord. The cervical and lumbar nerves have the largest roots, the caudal nerves the smallest. The number of spinal nerves is very large, there are at least fifty pairs. The spinal cord is invested by the usual protective membranes. Transverse sections of the spinal cord show the usual histological structure; the shape of the spinal cord varies in different regions, as also the size of the cornua of the grey matter and the depth of the fissures; but a detailed description of those regional modifications does not appear to be important. One may, however, notice that in the caudal region, the spinal cord, as seen in transverse sections, becomes more and more flattened from above downwards and more like a long extended ellipse, that the ventral fissure is only slightly indicated, and that the grey matter gradually decreases in extent, more particularly as regards the cornua. This change in the shape of the spinal cord takes place gradually as one follows its course posteriorly, until at the extremity of the tail the transverse section is quite an ellipse, the grey matter is reduced to a small mass round the central cavity, and the dorsal and ventral horns are entirely absent.

For details regarding the histology of the spinal cord including the nerve roots, nerve fibres, and spinal ganglia, reference may be made to the work of Stieda and Hoffmann.

The Brain.

On the dorsal surface of the brain, the following parts come into view passing in the antero-posterior direction: the olfactory lobes, cerebral hemispheres, choroid plexus (situated between the posterior ends of the latter), optic lobes, cerebellum, medulla, and the roots of several of the cranial nerves. On the ventral surface, the cerebral hemispheres extend far posteriorly and meet the medulla; the parts exposed are, in their order, the olfactory lobes, cerebral hemispheres, thalamencephalon with the optic chiasma and the hypophysis, the optic lobes, and the medulla oblongata. The roots of the twelve cranial nerves are also exposed. The lateral view supplements observation from the dorsal and ventral aspects, but more especially of the manner in which the medulla is prominently arched towards the ventral surface.

It appears superfluous in this work to describe the structure of the brain of the tortoise, as the fundamental morphology is similar to that occurring in fishes and amphibia, but a few points, which are to some extent characteristic of the brain of Chelonia, may be briefly indicated. A definite cortex occurs containing the special pyramidal cells such as are present in the pallium of all

the higher Vertebrata. The posterior parts of the cerebral hemispheres are, in connection with the development of the hippocampus, extended into lobi temporales. A small thickening in the region of the foramen of Munro represents the anterior pallial or hippocampal commissure, and there is also a trace of a posterior pallial commissure or fornix. The commissures, as a whole, are significant in relation to their greater development in the higher Vertebrata. The choroid plexi are very distinct in the Chelonia. The cerebellum has a thicker median portion, and thinner lateral parts, which are regarded as forming an approach to the differentiation in higher Vertebrata into the median vermis and lateral flocculi. There is not a pons varolii, and thus no sharp distinction between the cerebellum and the medulla. A marked feature of the posterior part of the brain of the tortoise is the convex curvature directed ventrally, which commences at the mesencephalon and continues posteriorly to the commencement of the spinal cord.

Cranial Nerves, Origin of the Paired Nerves from the Brain.

I. The olfactory nerve passes from the apex of each olfactory lobe, and divides immediately into two branches which extend anteriorly, closely adjacent to one another.

II. The optic nerve—the optic tract passes on the latero-ventral surface of the thalamencephalon towards the median line, where it meets the tract of the opposite side and forms the optic chiasma, from which the optic nerves proceed peripherally.

III. The oculo-motor nerve originates on the median ventral surface of the mesencephalon, *i.e.*, from the crura cerebri.

IV. The pathetic or trochlear nerve comes into view as a very fine slender nerve between the mesencephalon and the cerebellum.

V. The trigeminal nerve has strong roots on the lateral surface of the medulla, adjacent to the cerebellum; the gasserian ganglion is situated at the roots.

VI. The abducens passes out as a small trunk from the ventral surface of the medulla, near the medio-ventral groove; it lies in the same line as the auditory nerve, but more medianly.

VII and VIII. The facial and auditory nerves. These nerves originate from the medulla close together, near the margin of the fourth ventricle, slightly posterior to, but more dorsal than, the root of the trigeminal nerve. Associated with the auditory nerve is a small ganglion—the ganglion acusticum or vestibulare.

IX. The glossopharyngeal proceeds from the medulla slightly posterior to the base of the auditory nerve, and at a similar vertical position; it also has a small ganglion.

X. The vagus originates behind the glossopharyngeal as a number of minute bundles.

XI. The spinal accessory is a slender nerve trunk, which is formed from numerous extremely fine roots, originating from the medulla.

XII. The hypoglossal originates by three minute roots in close association with the roots of the spinal accessory.

Nervus Terminalis.

Two embryos of the turtle, *Emys lutaria,* were studied by Johnson, with special reference to the nervus terminalis and a comparison with that of Mammals. Its root is situated in Emys "on the medial surface of the hemisphere caudal to the bulbus olfactorius. It has ganglia in several clumps on the trunk and rami, and is distributed to the rostral part of the medial diverticulum of the nasal sac."

In his summary he writes, "in embryos of the turtle, pig, sheep, and man there is found a true nervus terminalis consisting of a ganglionated nerve whose root enters the telencephalon caudal to the bulbus olfactorius."

Peripheral Nerves.—Distribution of the Cranial Nerves. (*Pl. 40, figs. 1 and 2.*)

I. *Olfactory nerve.*—Processes from the neurones occurring all over the dorsal surface of the olfactory lobes unite to form small bundles of nerves. The latter become collected into larger bundles, which extend anteriorly along the length of the olfactory lobe, and form the olfactory nerve. The nerve has two rami, an external and an internal. The branches terminate in the nasal mucous membrane.

II. *Optic nerve.*—The optic tract of either side passes from the mesencephalon to the thalamencephalon, partially encircles the latter, and then extends from in front of the tuber cinereum to the base of the brain. In its lateral course from the thalamencephalon, the tract is only attached to the latter, and does not receive any additional fibres from it. The optic tracts break up on the ventral surface of the brain into numerous small bundles, which cross from one side to another, and become interwoven, so as to form the optic chiasma. The two optic nerves then proceed directly peripherally and finally enter the retina.

III. *Oculomotor nerve.*—The course of the oculomotor nerve is similar to that in other vertebrata; after it has entered the orbit it gives off branches to the rectus superior, rectus inferior, rectus internus, and obliquus inferior muscles.

IV. *Pathetic* or *trochlear.*—According to Stieda the roots of this nerve originate from a trochlear centre as a number of small bundles of medullated nerve fibres, which proceed from the ventral to the dorsal surface in a curve. When the small bundles leave the ventral surface they combine on each side to form the nerve, which appears on the dorsal surface of the brain between the cerebellum and the optic lobes. After the pathetic nerve has entered the cavity of the orbit, it proceeds to the superior oblique muscle.

V. *Trigeminal.*—According to Stieda the trigeminal nerve receives its fibres

from different parts of the brain; there is, firstly, a part of the root which appears to be the direct continuation of the superficial and peripheral longitudinal tracts of nerve fibres, and apparently corresponds with the sensory root of the trigeminal nerve of Mammalia; secondly, a part in which the nerve fibres originate directly from the neurones of the trigeminal nucleus; and, thirdly, a part originating from those obliquely directed bundles, which pass towards the central longitudinal bundles and are traceable to the commissure on the floor of the ventricle. Associated with the last root there is a small longitudinal bundle, which is reflected back in a curved manner into the course of the rest of the trigeminal. The trigeminal expands almost at once into the small flattened gasserian ganglion, from which there pass off (*a*) the ophthalmic, (*b*) the maxillary, and (*c*) the mandibular branches (Emys, Testudo). In addition to these three branches there is a fourth, which, arising as a very fine nerve, passes anteriorly into the orbit beneath the ophthalmic branch, and gives off branches into the superior and inferior depressor palpebrae muscles.

The ophthalmic branch (Pl. 40, fig. 1) is the smallest of the three branches of the trigeminal; it gives off (1) a frontal, (2) a nasal, and (3) a ciliary branch to the ciliary or oculo-motor ganglion. The frontal branch runs in the upper part of the eye-ball and above the superior oblique muscle, and innervates the nictitating membrane and the harderian gland. The nasal branch passes between the fibres of the retractor muscle of the eye, and then proceeds to the ethmoidal region and to the nasal cavity.

The maxillary ("supra-maxillary") branch leaves the cranium along with the mandibular ("infra-maxillary"); it has the following branches:—(*a*) the zygomatic which passes into the bony canal of the post-frontal; (*b*) the lacrymal, to the lacrymal gland; (*c*) the ramus communicans, connecting with the palatine branch of the facial, which passes to the pterygo-maxillary muscle; (*d*) the anterior palatine; (*e*) the posterior palatine; and (*f*) the infra-orbital, which passes through the palato-nasal foramen, gives off several posterior nasal branches, of which one branch connects with a small branch of the palatine and finally passes to the upper jaw; (*g*) the supra-maxillary or maxillary proper passes to the lower wall of the optic capsule. The third branch of the trigeminal, the mandibular ("infra-maxillary"), is the most important; it has the following minor branches:—(*a*) the temporal branch, which supplies the occipito-squamoso-maxillary muscle (M. temporalis); (*b*) the pterygoid, which innervates the pterygo-maxillary muscle (M. pterygoides); (*c*) the buccal branch, which extends between the temporal and pterygoid muscle, and then passes to the angle of the mouth; (*d*) the infra-maxillary branch (*ramus alveolaris*, Bojanus), which passes to the lower jaw; (*e*) the mylohyoid branch, which after passing through a canal in the lower jaw, passes to the intermaxillary or mylohyoid muscle.

VI. *Abducens.*—This nerve is, according to Stieda, very similar in its relationship to the ventral roots of the spinal nerves. It usually consists of three small root bundles, which lie successively the one behind the other. These come out directly from the small group of cells known as the abducens nucleus,

pass almost vertically through the white matter, and leave the medulla a short distance from the median line. The abducens passes into a special bony canal in the basisphenoid and then into the optic cavity, where it divides into two branches, one of which innervates the external rectus and the other by several branchlets the retractor oculi muscle.

VII. *Facial.*—The facial and auditory (VIII) are as usual closely associated. The roots of the facial nerve of Chelonia, Lacertilia, and Crocodilia, as contrasted with the roots of this nerve in many fishes and amphibia, are more completely separated from the roots of the trigeminal nerve. After the facial has penetrated the prootic, it passes into a special bony canal of its own, and then expands into a very minute ganglion. From the ganglion there proceed two main branches, an anterior, the palatine branch of the facial (*Ramus Vidianus ad facialem* of Bojanus), and a posterior which is a continuation of the facial itself. The palatine branch of the facial receives near its origin from the latter a sympathetic nerve branch (*Ramus Vidianus ad sympathicum,* Bojanus), the constituent parts of which originate partly from the glosso-pharyngeal, partly out of the carotid canal as the continuation of the sympathetic marginal trunk; it then proceeds into the bony canal situated between the basi-sphenoid and pterygoid (*canalis vidianus* of Hoffmann) and gives off posterior nasal branches. After emerging from the canal it anastomoses with the ramus communicans of the maxillary branch of the trigeminal nerve.

After the facial nerve has given off the palatine branch from the ganglion it proceeds further in its own canal towards the exterior, then it passes posteriorly over the columella and is connected by a loop with the petrosal ganglion and also with the chief cervical ganglion, which is situated close to the glosso-pharyngeal nerve; it then innervates the M. squamoso-maxillaris and the M. dilatator tubae, and small branches also pass to the M. sphincter colli (*latissimus colli,* Hoffmann). The facial is apparently not well developed in the Chelonia, for whereas in the higher Vertebrata it acts chiefly as the motor nerve of the muscles of the face, in the Chelonia, as there is a hard covering of scales on that part, this function is relatively reduced. It has even been doubted whether the facial in the Chelonia has a definite root of its own, distinct from the auditory; it has no special nerve endings, and has become connected with the development of the sympathetic nerve. It may be said in a general way that the facial plays a subordinate rôle in the Chelonia to that which it does in the higher Vertebrata.

VIII. *Auditory.*—This nerve is relatively complicated, for roots from very different parts of the medulla enter into its course. Three roots have been distinguished, namely:—the dorsal or posterior, the ventral or anterior, and the so-called facial root. The dorsal root is situated near the upper margin of the lateral wall of the fourth ventricle; its tracts of fibres pass through the white matter and divide at once at the entrance into the grey, one half passing anteriorly, and another passing posteriorly. The dorsal auditory nucleus commences at the part where the root fibres diverge from each other; in this small bundles occur, which are detached from the posteriorly directed root

bundle of the auditory nerve. Stieda was unable definitely to determine whether or not all the fibres of the posteriorly directed bundle enter into connection with the cells of the dorsal auditory nucleus, nor could he ascertain the exact course of the anteriorly directed longitudinal bundles.

The ventral or anterior root of the auditory nerve is more strongly developed than the dorsal or posterior root; it consists of numerous smaller bundles which pass through the white matter beneath the dorsal root, that is to say nearer the base of the medulla oblongata, and then enter directly the ventral auditory nucleus, from which branches spread out in all directions. In addition to these two true auditory roots, there is the so-called "facial root" which dips laterally from the central fibrous bundle behind the root of the auditory as a closed fibrous tract: it extends a fairly long distance anteriorly, then curves laterally, penetrates the lower auditory nucleus, and passes out of the medulla either with or in front of the most anterior of the auditory bundles. Stieda was unable to trace the facial root to a definite group of cells.

Peripherally, the auditory nerve divides into a vestibular branch to the utriculus and semicircular canals and a cochlear branch to the lagena.

IX. *Glossopharyngeal.*—The origin of the glossopharyngeal is similar to that of the vagus and spinal accessory (X–XI) nerves. Small root bundles extend slightly obliquely through the white and grey matter of the medulla, but it is not exactly clear from which group of cells these roots are derived; this also holds for the accessory and vagus nerves. As a rule, the glossopharyngeal is a very slender nerve. It passes out at the posterior end of the prootic into a canal of its own, and, after it has run through and emerged from the latter, it expands into a small ganglion, the ganglion petrosum. This ganglion is connected by two small branches with the ganglion of the root of the vagus nerve, as well as by another branch with the palatine branch of the facial nerve, and with the sympathetic nerve. As the palatine branch of the facial nerve anastomoses with the ramus communicans of the maxillary branch of the trigeminal, the glossopharyngeal is in indirect connection with the trigeminal. The trunk of the glossopharyngeal nerve divides beneath the Ganglion petrosum into two main branches, an anterior and a posterior. The anterior branch is the largest; it passes downwards in a curve and anteriorly along the vocal cords, between the larynx and the hyoid muscle, and becomes lost with its branches in the membrane of the base of the tongue; it gives off at the same time a pair of small branches to the laryngeal muscle. The main posterior branch is smaller than the last, and is distributed to the hyo-maxillary muscle. The Ganglion petrosum appears to occur in all Chelonia and probably in all Reptilia.

X, XI. *Vagus and Spinal Accessory.*—The origin of the vagus nerve is not distinct from the most anterior of the bundles of the roots of the spinal accessory, and it has been held that these should be taken together and the latter termed accessorio-vagus nerve. According to Stieda, the individual root bundles penetrate the white matter obliquely in a postero-anterior direction, and then sink into the grey matter.

The trunk of the "accessorio-vagus" nerve expands at about an inch from its origin into an oval swelling, the ganglion of the root of the vagus nerve. It is connected with the chief cervical ganglion by a slender branch just beneath the former ganglion. Vogt describes this branch as follows:—About a line beneath the point, where the vagus gives off the two supplementary branches already mentioned in connection with the glossopharyngeal, a smaller branch leaves the posterior surface of the trunk and turns towards the anterior muscles of the cervical part of the vertebral column. The root trunks of the hypoglossal nerve cross this branch, and the latter runs straight posteriorly to the carapace, and has a distinct connection with the first cervical nerve, but Vogt was unable definitely to trace such a connection with the second cervical and the true hypoglossal. After it has come out from under this nerve, the branch pursues its course, close to the muscles of the neck, and finally becomes lost in these, adjacent to the commencement of the first cervical ganglion, at the place where the first connecting loop passes off between the vagus and the sympathetic. There is, consequently, no connection by this posterior branch between the vagus and first cervical nerve with the sympathetic.

The trunk of the "accessorio-vagus" nerve immediately after its exit from the cranium gives off the Ramus accessorius (*Ramus muscularis n. accessorii ad m. sternomastoideum,* Bojanus; *Ramus accessorius,* Fürbringer), which proceeds posteriorly, and at the level of the second cervical vertebra (Emys) or third cervical vertebra (Testudo) passes into the internal surface of the M. capiti-plastralis by one or two branches, while its terminal branch anastomoses with the third and fourth cervical nerves.

The trunk of the "Accessorio-vagus" nerve is, at the place where the branches mentioned pass off from it, enclosed along with the hypoglossal and glossopharyngeal in a common sheath in such a manner that the glossopharyngeal is anterior, and the hypoglossal at first posterior then anterior and external, while the vagus turns away more posteriorly and beneath it, to follow the course parallel to the long axis of the neck, which must necessarily be crossed by the hypoglossal, as the latter passes directly ventrally and externally towards the cornua of the hyoid. At this crossing place, the main trunk of the sympathetic also proceeds posteriorly beyond the two nerves, and receives a very minute branch at this point from both the vagus and the hypoglossal. The vagus now turns towards the carotid, and follows this ventrally towards the pectoral girdle, but before it extends beneath the latter, it gives off:—

(1) The pharyngo-laryngeal branch which soon divides into two, namely (*a*) the laryngeal branch to the trachea, (*b*) the pharyngeal branch to the œsophagus.

(2) The recurrent branch, which originates at a very pointed angle from the vagus at about the middle of the neck; it turns over the carotid, passes internally towards the trachea, and comes to lie at the side of the latter, in which, and in the adjoining parts, it branches extensively, and can then be traced to the larynx. Several lines further down, a loop-like connecting branch

passes off in a gently inclined arch as viewed posteriorly, towards the first ganglion of the sympathetic nerve. The nerve then proceeds beside the carotid towards the thoracic viscera until it arrives at the aortic arch, when it gives off (*c*) the cardiac branches, which consist partly of a complicated plexus of fibres above the pericardium. These arise on the one hand from the trunk of the accessorio-vagus nerve, on the other hand from the first thoracic ganglion of the sympathetic, and are probably analogous with the cardiac plexus. Finally, the trunk of the "accessorio-vagus" nerve gives off (*d*) the pulmonary branches, and (*e*) the œsophageal and ventricular branches.

XII. *Hypoglossal.*—The hypoglossal arises in a similar way to the ventral roots of the spinal nerves. Its slender roots pass obliquely through the white matter, and enter the ventral cornua of the central grey matter. The point of entrance is, however, higher than those of the ventral roots of the spinal cord, namely, high up, at the medial margin of the ventral horn. The root fibres of the hypoglossal extend into the grey matter quite close to the inferior commissure, several appear to combine beneath the tracts of the inferior commissure. The roots pass externally through two special foramina in the exoccipitals, and run obliquely posteriorly and ventrally. Outside the skull, the two branches unite into a common trunk, and receive two branches, much stronger than themselves, from the first and second cervical nerves. The point of union with these last two branches is also the point where the hypoglossal crosses the vagus. The nerve then curves so as to lie nearer the glossopharyngeal, and soon divides into three branches, namely :—

(*a*) Ramus colli descendens, which accompanies the accessorio-vagus nerve as far as the fifth cervical nerve, and then passes to the M. coraco-hyoideus.

(*b*) Ramus hypoglossi anterior to the M. hyo-glossus and genio-glossus and in *Emys europaea* according to Bojanus to the sublingual gland.

(*c*) Ramus hypoglossi posterior to the M. genio-hyoidens.

Sympathetic Nervous System.

The first fibres of the head trunk originate from the trigeminal nerve. They proceed from the latter as the sphenoidal plexus to the infra-orbital nerve, and form, after they have united together, a thin cord which passes posteriorly on the ventral wall of the optic cavity and follows the direction of the long axis of the skull.

According to Vogt's investigations the sympathetic then passes into a deep canal in the prootic, inside which it curves round the auditory organ, and later leaves the bone by a special aperture above the articulation of the lower jaw. This anterior head trunk of the sympathetic apparently corresponds with the Nervus Vidianus. After the nerve has become free from the bone it pursues its horizontal but posteriorly directed course a short distance further, passes away beneath the glossopharyngeal, and receives, as it proceeds between the carotid on the inside and the vagus and hypoglossal on the outside, the nerve trunk which Vogt termed the superior head trunk of the sympathetic ("oberen

Kopf stamm des Sympathicus"), the latter resulting from the union of the "ramus communicans" of the facial nerve with a small branch of the glossopharyngeal. At the point of union of these two head trunks of the sympathetic nerve, which is just at the place where the vagus and hypoglossal cross, the combined trunk receives a connecting branch from the vagus and hypoglossal, the course of which renders the dissection of this region very complicated, and tends to conceal the relationship between the cranial nerves already mentioned and the sympathetic cord. After receiving these various branches the trunk, which is now of considerable size, pursues its course towards the pectoral girdle, without giving off any branches during its course, but receiving branches from the upper cervical branch of the vagus, and gradually increasing in thickness as it proceeds.

The first ganglion is formed, according to Vogt, shortly before the cord passes beneath the pectoral girdle. It is an elongated spindle shape, but fairly thick, and lies along the lateral curve of the neck. Three branches enter at its anterior end, namely, the sympathetic trunk, the last branchlet of the posterior branch of the vagus, and a fairly important branch which has come from the vagus a little higher up, and which bends round in a loop-like curve towards the ganglion. According to Vogt no nerves come off from the upper surface of the ganglion, but all the more out of the lower surface, which gives off probably about ten to fifteen fibres, which anastomose a great deal, and become interwoven with the branches of the vagus, forming a complicated plexus which sends off branches to the pericardium, heart, and adjoining viscera situated at the commencement of the thoracic cavity.

The posterior pointed end of the ganglion elongates into a short nerve trunk, and soon becomes absorbed, according to Vogt, in aberrant structures which have been said to occur only in the Chelonia. These are three large ring-shaped ganglia, situated successively the one after the other, which are apparently formed by the converging and diverging of separate branches; but these rings are very large and thick, and their joints are distinctly of a ganglionated nature, and they differ markedly from the other nerve trunks in thickness, non-uniformity, greyish-red colour, and softer texture.

Nerve links pass from the ring-shaped parts and from the ganglionated connecting parts to the brachial plexus, and connectives also proceed from the nerves of the plexus to the ganglionated chain, which, according to Vogt, consists of only three parts, and these become absorbed further posteriorly in the usual branchlets passing over from the root of one nerve to the root of another, which represent the abdominal part of the sympathetic nerve.

The sympathetic of Chelonia, therefore, consists of two trunks, namely, the anterior head trunk which arises from the trigeminal and the superior head trunk which originates from the glossopharyngeal; the trunk thus originating from the union of the two then receives further branches from the accessorio-vagus and hypoglossal, and, lastly, from the posterior cervical trunk, which derives its primary fibres from the vagus (mainly) and first cervical.

Bojanus distinguishes the following plexi in *Emys europaea*:—(*a*) Plexus

cardiacus; (*b*) Plexus aortae sinistrae; (*c*) Plexus coeliacus; (*d*) Plexus aortae descendens; (*e*) Plexus renalis; (*f*) Plexus arterias hypogastricae; (*g*) Plexus sacralis.

The Spinal Nerves. (*Pl. 39.*)

It is recommended that a dissection of the spinal nerves be made by the following method:—

A large specimen is killed by placing cotton wool saturated with chloroform in the pharynx; the carapace is then repeatedly dipped in boiling water, after which the horny shields can be readily removed with a rough scalpel. The carapace is then inverted in a vessel containing diluted hydrochloric acid, and after twenty-four hours or so the carapace will have become decalcified and can easily be peeled off from the entire dorsal surface. The spinal nerves are then seen running transversely on the underlying membrane parallel with the transverse intercostal blood-vessels anterior and posterior to them.

Cervical Spinal Nerves.

It has already been mentioned that the spinal nerves, with the exception of the first and second, have, as is usual in the Vertebrata, two roots, a dorsal and ventral. The first two cervical nerves, which have only ventral roots, are poorly developed; they pass to the small anterior cervical muscles. The first cervical nerve leaves the cord between the basioccipital and the first cervical vertebra, the second nerve between the first and second vertebra, and so on with the other spinal nerves in succession.

Spinal Nerve III. The ventral branch of the third spinal nerve ramifies in the dorso-occipital muscle; the dorsal ramus chiefly innervates muscles in connection with the head, neck, and carapace.

Spinal Nerve IV. The ventral branch innervates the dorso-occipital and the long muscle of the neck, and passes finally to the muscle of the carapace, scapula, and acromium process: the dorsal branch innervates two muscles of the carapace, head, and neck.

Spinal Nerve V. The ventral branch passes to the long muscle of the neck and the cervico-squamosal muscle; the dorsal branch has a similar course to that of the fourth.

Spinal Nerves VI–IX.—Brachial Plexus. The ventral branches of the sixth, seventh, eighth, and ninth nerves form the brachial plexus, the branches of which innervate the pectoral muscles and those of the anterior limb. The participation of only the posterior cervical nerves in the formation of the brachial plexus appears at first sight to constitute a characteristic feature of difference from the Amphibia, but this is really brought about by a structural difference, for, although the serial number is different in these two groups, the brachial nerves are similarly related to one another, and the individual nerves which pass peripherally from the plexus proceed in a like manner. The contrast consists in the difference in the number of cervical nerves which are situated anterior to the brachial plexus, and are not connected with it, namely, one or

two in the Amphibia, five in the Chelonia, and this is in correlation with the increased number of vertebrae in the neck of Chelonia.

Dorso-lumbar Nerves I–VII.—Spinal Nerves X–XVI. The dorso-lumbar nerves may either be traced from the dorsal or from the ventral surface. If from the former, the carapace is decalcified and peeled off when the nerves are conspicuously exposed. If from the latter surface, the greater part of the alimentary canal, the reno-reproductive organs, and the lungs are removed. The dorso-lumbar nerves are seen running transversely underneath the carapace. These nerves, running in the trunk region, are, speaking generally, in connection with the muscles of this region, namely, the M. obliquus abdominis, transversus abdominis, dorso-occipitis, longissimus dorsi, diaphragmaticus, and with the plastron.

Dorso-lumbar Nerve I—Spinal Nerve X. This nerve emerges posterior to the first dorsal vertebra; its chief branches are a subcostal running transversely underneath the second costal plate, and a dorsal branch to the subclavian muscle.

Dorso-lumbar Nerve II—Spinal Nerve XI. This nerve has the following branches:—(1) the subcostal running under the carapace to the plastron; (2) a branch to the interior of the third costal plate; and (3) a slender filamentous nerve connecting with the sympathetic.

Dorso-lumbar Nerve III—Spinal Nerve XII. The dorsal branch runs to the Musculus longissimus dorsi, also communicating through a plexus with the sympathetic; other branches, a subcostal running underneath the third costal plate to the plastron, and one to the interior of the costal plate as in the third dorso-lumbar nerve.

Dorso-lumbar Nerve IV—Spinal Nerve XIII. The subcostal ramus runs beneath the fourth costal plate to the plastron; a second ramus passes into the costal plate, and as in the previous nerves there is a connection with the sympathetic.

Dorso-lumbar Nerve V—Spinal Nerve XIV. The subcostal branch to transverse and oblique abdominal muscles, and a branch terminating in the fifth costal plate.

Dorso-lumbar Nerve VI—Spinal Nerve XV. (1) A subcostal branch running internal to the sixth costal plate to the transverse and oblique abdominal muscles; (2) a branch to the interior of the sixth costal plate; (3) a connection with the subcostal of the seventh nerve.

Dorso-lumbar Nerve VII—Spinal Nerve XVI. (1) A subcostal branch to the same muscles as the preceding, (2) a branch to the interior of the carapace, (3) a posterior ramus to the lumbo-sacral plexus, (4) a connecting branch with the sympathetic.

Lumbo-sacral Plexus.

Dorso-lumbar Nerve VIII—Spinal Nerve XVII. Two upper branches mainly to abdominal muscles, a third branch, the obturator nerve.

Dorso-lumbar Nerve IX—Spinal Nerve XVIII. Three branches, namely,

(1) the crural nerve, (2) a connecting branch with the obturator of the eighth nerve, (3) a connecting branch with the tenth dorso-lumbar nerve.

Dorso-lumbar Nerve X—Spinal Nerve XIX. Nervus furcalis of v. Ihering, with a branch to the ischiadic nerve and a fork, which divides to form a root for the crural and another for the obturator nerve.

Muscular System.

The reader might be referred to the figures by Bojanus, but it is very difficult to procure that classic work (1819). Hoffmann has given modifications and reproductions of the figures by Bojanus, and detailed descriptions of the course of the muscles; his work is more accessible. Fürbringer has also given a very good description of the muscles of the pectoral girdle, and therefore it appears to the author that it would be a redundance to deal with this system, but several conspicuous muscles may be mentioned.

Pectoralis major.—When the plastron has been removed, the pectoralis major is seen on each side with anterior and posterior portions, both converging to their insertion on one of the tuberosities of the humerus.

Rectus Abdominis.—A fan-shaped muscle near the pelvis, the origin of which from the plastron is divided on removing the latter, with anterior fibres running backwards and posterior fibres running forward to be attached to the large process on the antero-lateral margin of the pubis.

M. obliquus abdominis and M. transversus abdominis.—Retractor muscles of the Head and Neck.

The great retractor muscles of the head and neck, of which there are four on each side, extend from the bodies of the dorsal vertebrae, the one which extends furthest forward having its origin farthest back. These muscles extend anteriorly to the posterior part of the skull and to the cervical vertebrae.

Protractors of the Head and Neck.—These extend from the carapace and pectoral girdle to the head and neck.

Bojanus, Hoffmann, Götte, Fürbringer, and others have described and figured the course of the distribution of more than one hundred and twelve muscles in the Chelonia. In connection with the nomenclature of the muscles, Hoffmann regarded the anterior section of the pectoral girdle (the acromium process) as the clavicle; therefore, instead of, for example, Musculus testo-scapulo-clavicularis, one would read Musculus testo-scapulo-acromialis.

Section 11.—Sensory Organs.

Olfactory Organs—Stato-auditory Organs—Eyes—Accessory Glands.

Olfactory Organs.

The external narial apertures are situated in the Chelonia very closely adjacent, dorsal, and external to the median parts of the upper jaws. Each

aperture leads into a canal which widens out posteriorly in a funnel-like manner, and passes over dorsally into the spacious olfactory cavity and ventrally into a space, the choanal cavity, lined with ordinary epithelium. The choanal cavity is continued posteriorly into the choanal canal, which is formed by the meeting of the margins of a palatal groove, while at the same time the palatal lamina unites medially with the projection of the vomer. The choanal canal communicates posteriorly with the pharynx at the secondary choana, which adjoins that of the other side (*vide* diagrams of olfactory organs of Testudo by Plate, fig. 304, F. & G.). A large, external nasal gland opens into the anterior chamber. The concha is only differentiated as a shallow ridge projecting towards the nasal cavity.

In a figure of a transverse section through the posterior portion of the olfactory organ of *Testudo graeca*, by Plate, fig. 311, one sees the organ bounded above by the prefrontal, maxilla and premaxilla; the dorsal nasal cavity or pars olfactoria; the ventral or choanal cavity comparable with the pars respiratoria. The wall of the first cavity has a sensory epithelium, while that of the second has, as in other Vertebrata, only a respiratory epithelium. On the medial wall of the choanal cavity there is a groove with a sensory epithelium, which is regarded as a very primitive form of Jacobson's Organ. The part is innervated by a branch of the olfactory nerve. In connection with the groove, and slightly dorsal to it, there is a small gland—the median nasal gland—which may be homologous with Jacobson's gland in Amphibia. In Emys the epithelium of Jacobson is much better developed than in Testudo, and lines the greater part of the entire choanal cavity as a dorsal, ventral, and anterior projection. Small glands, Bowman's Glands, occur on the dorsal and lateral walls of the olfactory part of the organ internal to the olfactory epithelium. A lacrymal duct does not occur in the Chelonia, and its absence is perhaps to be correlated with the aquatic life of some, at least, of the primitive forms.

It appears unnecessary to repeat the admirable figures given in Plate's "Die Sinnesorgane der Thiere."

Stato-auditory Organs.

The stato-auditory organ shows the same fundamental structure throughout the Vertebrata with the exception of Fishes, and is specially interesting as presenting in a series of stages a progressive evolution in Amphibians, Reptiles, and Birds of a specialised part for hearing, which reaches its fullest differentiation in the cochlea of the Mammalia. The vesicle of the ear has the usual two chambers, a larger, superior part, the utriculus, and a smaller inferior, the sacculus. From the utriculus there pass off the three semi-circular canals, which are characteristic of the static part of the ear of the Vertebrata. These canals expand into ampullae at the lateral connections with the utriculus. On the internal walls of the utriculus, sacculus, and ampullae there are special sensory end-plates which are of great functional significance. In all Vertebrata there is an invagination of the sacculus, termed the lagena, which is small and

unimportant in Fishes, but from which in most Amphibia, Reptiles, Birds, and Mammals there has separated off a papilla—the papilla basilaris—which in Crocodiles, Birds, and Monotremes is slightly curved, but in higher Mammals is a spiral organ—the specialised part for hearing, or cochlea.

The sensory terminal plates of the stato-auditory vesicle develop from a common basis, for at a very early stage in development the originally one-layered epithelial lining of the vesicle becomes thicker and several-layered at its medial wall. From the latter, parts are gradually differentiated which become the sensory terminal plates of the vesicle of the adult.

In Selachians, Teleosteans, and some Urodelan Amphibians, there are seven of these sensory terminal plates in each labyrinth, namely the comb-shaped crista in each of the three ampullae, a macula utriculi and macula neglecta in the utriculus, a macula sacculi and a knoblike evagination, called the papilla lagenae, in the sacculus. In the Salamandrian, Coecilian, and Anuran Amphibia, in Reptiles, Birds, and Monotremes, there are eight (or nine with the double macula neglecta) sensory terminal plates, as a small papilla basilaris has separated off from the papilla lagenae. In higher mammals, on the other hand, a reduction to six has taken place, as the macula neglecta and papilla lagenae have disappeared. The papilla basilaris, on the other hand, enlarges very greatly, and while it is only slightly curved in Reptiles and Birds, becomes in Mammals the well developed spiral or cochlea containing the auditory cells in that part known as the organ of Corti.

Hesse has given a very interesting comparative diagram of the left labyrinth of the following:—

(*a*) Teleost, (*b*) Frog, (*c*) Tortoise, (*d*) Crocodile, (*e*) Bird, and (*f*) Mammal. In the labyrinth of the Teleostean fish the Macula utriculi, the Macula sacculi, and the Papillae lagenae are differentiated; in that of the Frog, in addition to those three, there has been separated off the Papilla basilaris, lying beside the Papilla lagenae. A further stage in evolution is attained in the Chelonia, as in this case the Papilla basilaris has become a short canal-like part with the papilla lagenae near its base. The macula sacculi of Chelonia is very long as compared with that of the Crocodile, Bird, and Mammal. In the Crocodiles, the papilla basilaris has become much longer, and the papilla lagenae is at its extremity; that of birds is similar, except that in them the papilla basilaris has become more curved. In the Mammalia, the conspicuous features are the macula utriculi, macula sacculi, and the very long curved papilla basilaris or cochlea (the papilla lagenae having disappeared).

The sound-conducting part of the Chelonia is very similar in general structure to that of the Frog and other Anuran Amphibia. The similarity is dependent on the fact that the two are derivable from a similar evolutionary stage.

The tympanum, which is very large in the Chelonia, is on or near the surface, and lies in a ring bounded by the squamosal and quadrato-jugal.

The columella consists of two pieces, namely, a large internal bony stapes

(plectrum), which enlarges at its inner end and closes the foramen vestibuli, and a small external cartilaginous extra-columella, which is applied to the tympanic membrane. The stapes and extra-columella are fused in the Chelonia. In most terrestrial tortoises, the tympanic membrane is thick and covered by the ordinary skin. A section through the auditory canal of a tortoise shows the skin and tympanic membrane, within that a large tympanic cavity which is crossed by the extra-columella externally and the stapes internally; the tympanic cavity enlarges dorsally beneath the squamosal bone into an auxiliary cavity, and ventrally it communicates by means of the Eustachian tube with the mouth. The internal end of the stapes connects with the sacculus of the inner ear, dorso-lateral to the outer part of which lie the opisthotic and quadrate bones. Comp. Fig. 180, p. 191 in Plate's "Die Sinnesorgane der Thiere." Hasse (1873) gave a detailed description of the structure of the auditory organ and adjacent parts of the skull in *Chelone midas*.

The Eyes of Chelonia.

In a general way, it may be said that the eyes of Chelonia are essentially characteristic of terrestrial creatures as contrasted with the lower aquatic Vertebrates. Corresponding with the terrestrial mode of life and the consequent exposure of the eyes to dangers and to dust, etc., we find that the upper and lower eye-lids are thick and well-developed. In addition to the usual six muscles of the eye, there is a retractor bulbi muscle. In the ciliary region, a bony ring is situated in the sclerotic layer. In the sclerotic of the basal part of the eye, there is a cartilaginous part, as in other Reptilia with the exception of the snakes. The rods in the retina, like those of other Reptiles with the exception of Crocodiles, are much fewer in number as compared with the cones. During accommodation, the soft lens changes its form, and it has laterally a circular ridge of raised epithelium. The position of the eye, like that of other Reptiles, is at the side of the head, and thus each has a field of vision independent of the other, or each has, at the most, only a small common area of sight. The size of the eye relative to that of the head is an average.

The ciliary body, like those of Crocodiles, has strongly developed radial folds. At the base of the ciliary body, internal to the bony ring, there lies a distinct ciliary muscle, which in contrast to that of Amphibia is in this case distinctly transversely striated, and contains meridional as well as circular fibres. This also occurs in other reptiles with the exception of snakes. As in Amphibia, a lens or transversal muscle occurs in Chelonia and Lacertilia in the ventral region of the ciliary body. This is missing in snakes and alligators.

The iris is shorter and thicker in Chelonia and Lacertilia than in Ophidia and Crocodilia, and variously coloured pigment cells are distributed in it. In a number of Chelonia, the iris is differently coloured in the different sexes. The muscles of the iris are all striated.

Accommodation depends, as we know, on a change taking place in the form

of the lens; in viewing near objects, the anterior and posterior surfaces of the lens become more arched than they are in the usual position. Hesse found that when the eye of the tortoise was stimulated electrically, a contraction of the ciliary body took place, during which the lens became somewhat constricted anteriorly, and, simultaneously with its becoming more arched in front, it was pushed further in the direction of the cornea and the posterior surface also became more strongly arched. During these changes, the sphincter muscle of the iris seems to play the chief part.

The Eye-lids.

The eye-lids of the Chelonia like those of most other Reptiles are three, namely (1) a small slightly movable upper eye-lid, (2) a much larger more mobile lower eye-lid; both resemble the ordinary scaly skin externally but have a soft layer containing goblet cells internally, and (3) a nictitating membrane originating from the anterior upper angle of the eye. In Crocodilia and Chelonia, the tendon of the nictitating membrane is continued into the nictitating membrane muscle (musculus pyramidalis) which arises from the median wall of the bulb, and proceeds above the optic nerve into the tendons. In the Chelonia, the muscle is connected with a second tendon in the lower lid. A musculus bursalis, such as occurs in Lacertilia on the posterior surface of the bulb, is not present.

Accessory Glands.

As in other reptiles, a harderian or nictitating membrane gland occurs at the anterior inner angle of the eye, and a lacrymal gland at the posterior outer angle.

The harderian gland has usually a more acinose, the lacrymal gland a more tubular structure, but this difference is not always marked. A further distinction is that the harderian gland is situated on the anterior and lower surface of the bulb and opens on the nictitating membrane, while the lacrymal gland is situated dorsally and opens on the internal surface of the upper lid at the temporal angle. In some Chelonia such as *Chelone midas*, the harderian gland is small, but the lacrymal gland is so large that it fills up most of the upper part of the orbit. In the Crocodilia, on the other hand, the reverse is the case, the harderian being much larger than the lacrymal gland. It has not been exactly determined, but probably these two glands have a similar function, namely that of facilitating the movements of the eye-lids. The lacrymal duct, which is present in the lizards and is quite rudimentary in snakes and crocodiles, is entirely absent in tortoises.

Section 12.—Development.

Development of the Turtle—Main Features in the Development of Chelonia.

The author was unsuccessful in several attempts to rear tortoises from the egg by means of artificial incubation; reference must therefore firstly be made to the very important early work, with numerous figures, by Louis Agassiz on the "Embryology of the Turtle" (1857).

Agassiz's descriptions and figures of the later developmental stages must still be regarded as fundamentally correct, although those of the earlier stages of segmentation and the formation of the germinal layers can scarcely be considered as in accord with the ascertained facts of modern embryology. Frequently, however, the apparent discrepancies are not so much due to actual differences in the observations made, as to diversity of nomenclature, thus, for example, the terms protoplasm, cytoplasm and blastodise were not then in use, the nucleus or germinal vesicle was termed the "mesoblast," the part of the cell surrounding the nucleus the "ectoblast," the nucleolus or germinal spot the "entoblast," and the endo-nucleolus the "entosthoblast." In his description of the growth of the embryo, Agassiz does not use the modern terms for the three germinal layers, epiblast, mesoblast, hypoblast, but speaks of an upper layer and a "subsidiary" layer, and it is not always quite clear in the further description of the development of the latter which part corresponds to mesoblast and which to hypoblast.

In spite of the differences in nomenclature, and the record of ideas regarding the early stages of development, which have since been found to be erroneous, Agassiz's description and figures of the development of the turtle are certainly well worthy of attention. The developmental processes of course show a general similitude to those of the chick.

The period of copulation in Testudo, as in other Chelonians, is prolonged, during which the male is partly carried on the back of the female. The eggs are laid in small numbers. They contain within hard, calcareous shells, a layer of albumen surrounding the yolk and blastodix, and are buried in the earth. The eggs of *Testudo graeca* and *ibera* are about the size of a pigeon's egg. They are very rarely hatched in England (see explanation of figures). According to Agassiz, the process of copulation in *Emys picta* takes place twice annually, namely in spring and autumn, from the seventh year onwards, and the first deposition of eggs in the eleventh year. There are thus four grades of maturing ova during this period. In this case then, there is a long duration within the parent followed by a lengthy life after hatching—a span of life in some Chelonians of a hundred and fifty to two hundred years.

The reader is referred to the extremely important papers on the development of Chelonia by Mitsukuri. It is beyond the scope of this work, more especially as regards figures, to give a sufficiently detailed account of his investigations.

It is well known that the ovum of the Chelonia has a very large amount of yolk (megalospheric egg), and that therefore the egg-segmentation is partial or meroblastic; it is confined to the cap of cytoplasm which lies at one pole on the large rounded mass of yolk or deutoplasm. Segmentation proceeds after the manner shown in Plate X of Agassiz, and results in the formation of the blastoderm lying on the surface of the yolk.

The first two divisions are meridional, but tangential divisions soon take place and the blastoderm becomes formed. The blastoderm then "consists of a superficial layer of flattened ectoderm cells, and underneath this, rounded, lower-layer cells which are separated by interstices containing fluid." According to Mitsukuri (as contrasted with Agassiz) the blastoderm is always found at the upper pole in whatever position the egg is placed. The blastoderm is pellucid, but an area becomes marked out in it by its greater opacity. This area is the embryonic shield, and its opacity is brought about by the ectoderm becoming thicker and its cells columnar. Near the posterior end of the shield on the dorsal surface is a crescentic transverse slit, which is the dorsal opening of the blastoporic passage.

The embryonic shield shows two zones arranged concentrically on the surface, an outer and inner, the latter being distinguished from the former by its greater opacity.

A longitudinal section at this stage (one hour after deposition of the embryo) shows the blastoporic passage, commencing at the dorsal surface, and leading obliquely forwards to the ventral surface. The cellular structure is very different in front of the blastoporic passage from that behind. In front of the passage there are only two layers, namely, the epiblast and the primitive hypoblast. The epiblast is a well defined sheet of cells extending far forward, consisting posteriorly of columnar cells and anteriorly of squamous cells, the latter in the anterior transparent part. The lower layer or primitive hypoblast consists in the anterior transparent area of a loose layer of cells containing numerous fine yolk granules; in front it passes into the bed of yolk in which nuclei occur. The primitive hypoblast when traced backwards becomes at first only two or three cells deep, and then suddenly becomes much thicker at the place corresponding with the anterior margin of the outer concentric zone, which is seen superficially on the embryonic shield. The hypoblast cells are at this place arranged in a loose network with large meshes. Further back the cells of the primitive hypoblast become columnar, and to some extent resemble the columnar epiblast situated above it at the blastoporic opening. It is thicker than the above, and is formed of several layers of cells. At the anterior dorsal lip of the blastoporic passage the primitive hypoblast is continuous with the epiblast (Mitsukuri, 1891, Pl. 3, fig. 5).

It has already been stated that the cellular structure is different behind the blastoporic passage. The epiblast is distinct in the hindmost part of this up to the blastoporic passage, but there it passes into a "large thick mass of cells" extending along the floor of that passage (Fig. 5a, Mitsukuri). The lower layer is continuous behind with the yolk mass, its cells contain numerous

yolk granules; it is also connected with the large mass on the floor of the blastoporic passage by "irregular reticulate strands of cells." The layers behind the blastoporic passage are therefore not so clearly separated, rather they are fused together, and this mass of cells apparently corresponds with the peristomal mesoblast (Rabl). "Eventually it will stretch backward for the space of 180° like an open fan between the epiblast and the definitive hypoblast."

Transverse sections of embryos (Clemmys) of the same age bring out other points. Thus, transverse sections taken directly behind the blastoporic passage show a structural arrangement of the cells—a median proliferation of cells—which is apparently the commencing primitive streak. A transverse section nearer the dorsal opening of the blastoporic passage shows "the large thick mass of cells," and it is at this part that later on the yolk plug becomes established (Fig. 22, Pl. 3, Mitsukuri). A transverse section through the front part of the ventral opening of the blastoporic passage shows the cells of the lower layer arranged in the middle line in a regular columnar epithelium, forming the chorda-hypoblast, which subsequently gives rise not only to the notochord but to a part on each side of the latter which "eventually becomes incorporated in the mesoblast." At the sides the chorda-hypoblast is continued into "loose irregular reticulate masses of lower-layer cells" containing numerous yolk granules. Further to the outside this lower layer becomes an extremely thin sheet over the pellucid area seen in surface view, and then it becomes continuous with the stratum of yolk.

The embryo at this stage is therefore composed of two layers, the epiblast and the primitive hypoblast; but besides these there is a hint of commencing mesoblast in the median mass of cells found behind and on the floor of the blastoporic passage, which is continuous with the two primary layers. In front of the blastoporic passage medianly the chorda-hypoblast is commencing to differentiate as columnar epithelium, which originates from the loose network tissue of the primitive hypoblast.

The next great steps in development consist in the more definite formation of the three germinal layers, epiblast, hypoblast, and mesoblast.

Originating from the thick mass of cells behind the blastoporic passage—peristomal mesoblast—a pair of mesoblastic bands becomes formed, one on either side of the median chorda-hypoblast, between the latter and the gut-hypoblast—this is the gastral mesoblast of Rabl.

Mitsukuri insists that "only the median part of what I have hitherto called the chorda-hypoblast gives rise to the chorda dorsalis, and that each side of it becomes eventually incorporated in the mesoblast."

A transverse section through the head region of Clemmys, three days old, shows the epiblast, the median chorda, from which the chorda-hypoblast proceeds upwards and laterally and becomes continuous with the mesoblastic mass, the gut-hypoblast also turns upwards and becomes continuous with the mass of mesoblast; a small cavity has appeared as a diverticulum of the archenteron between the chorda-hypoblast and the gut-hypoblast and has become surrounded dorsally by the mesoblastic mass. This section shows the same essential features

as a transverse section of Amphioxus—fig. 34, D; Kerr's Embryology—if one allows for differences due to the presence in the Chelonian of a mass of yolk, and to the fact that the archenteron is not yet shut off as it is in Amphioxus.

To summarise, when a transverse section is studied of a very early embryo of Clemmys (1–3 hours after deposition), at a point slightly in front of the blastoporic passage, the following are observed in the lower layer or primitive hypoblast: (1) median columnar cells, (2) lateral to those another set of cells, and (3) still further laterally a loose tissue. The fate of those three is that the first becomes the notochord, the second gets incorporated in the mesoblast, and the third becomes the gut or definitive hypoblast. In fact, there are comparable features to a transverse section of a very young Amphioxus.

At a very early stage the embryo consists of epiblast and primitive hypoblast, except in the region behind the blastoporic passage, where there is peristomal mesoblast. This mesoblast soon "increases in bulk, and spreads out in all directions like an open fan. From the two edges of this fan the formation of the gastral mesoblast proceeds forward." A patch of epithelium on each side of the rudiment of the notochord becomes subsequently the mesoblast. The rest of the primitive hypoblast forms the gut-hypoblast, but the patch of epithelium (gastral mesoblast of Rabl) proliferates and spreads outwards and upwards between the epiblast and the gut-hypoblast. At this stage the internal end of the latter on each side is some distance from the notochordal rudiment, but it soon extends inwardly towards the chorda, and in so doing shuts off the gastral mesoblast from the gut cavity. The inward extension of the gut-hypoblast is apparently the commencement of the process by which the chorda, the mesoblast, and the gut-hypoblast become independent of one another. This separation occurs in the middle of the embryo, but in the section further back the degree of separation becomes less and less marked until an indifferent condition is reached.

The following quotation is of special interest:—"These facts have also, in my opinion, an important bearing in explaining the mesoblast formation in the chick. Fig. 100 in Balfour's 'Comparative Embryology,' Vol. II, is substantially the same as Fig. 17 or 38 of the present paper. Now suppose that the earliest phases of the mesoblast formation are very rapidly gone through or altogether skipped over, and the stage represented in Figs. 17 and 38 is reached *per saltum*, we shall then necessarily obtain appearances which would make us conclude that the lateral plates of the mesoblast, or at least the part immediately adjacent to the chorda, become split off from the hypoblast. My contention then is that the process of the mesoblast formation in the chick is an extremely abbreviated form of the process described above in Clemmys or Trionyx."

Foetal Membranes of Chelonia.

Kerr (1919) has given a useful summary of Mitsukuri's very important work, "On the Foetal Membranes of Chelonia" (1890), with 88 figures and

7 diagrams; the latter are very important, as they afford a very valuable summary of the development of the foetal membranes in the Chelonia.

Appendix.—Practical Suggestions.

Method of killing.—Draw the head forward from the shell, force open the mouth, insert a pipette containing chloroform into the opening of the glottis at the base of the tongue, and drive chloroform into the lungs. This is a comparatively rapid method of killing the tortoise; a slower method is by thoroughly soaking a mass of cotton wool with chloroform, inserting this into the back of the mouth, and leaving it for at least twenty-four hours. When the animal no longer responds to any stimuli, thoroughly extend the neck, and keep it in the protracted state. The examination of the external characters and of the buccal cavity is then proceeded with (Pl. 32, fig. 6).

Dissection.—Saw through the bony bridges connecting the carapace and plastron. This should be done very carefully when the saw is nearly through, otherwise there will be much unnecessary loss of blood. Cut through the skin with scissors anteriorly and posteriorly, close to the plastron. Dissect away, with the scalpel, the soft parts attached to the dorsal surface of the plastron from before backwards, keep close to the bone and gently raise the plastron. As the plastron is gradually separated, note the ligaments passing from it towards the acromial processes of the pectoral girdle. When the plastron has been removed, note the parietal peritoneum and the attachments of a few muscles.

Cut along the anterior abdominal veins and ligature them; they pass dorsally to the liver, but receive branches from the pectoral region. Trace the anterior abdominal veins at this stage a slight distance posteriorly and laterally. Expose the viscera and heart.

The thoracic and abdominal viscera may be loosened by freeing the pectoral girdle, and to some extent the forelimbs; this can be done by placing your thumbs under the coracoid bones, turning both halves of the pectoral arch forward, and breaking the ligamentous attachment of the scapula to the carapace. Move the forelimbs backwards and forwards so as to loosen the attachments. Run water over the viscera and float out the organs. (Pls. 24, 25, 27, and 30.)

Dissection of the Veins (Pl. 34).—Unless the tortoise has been very slowly and carefully opened, the veins become empty, collapse and are difficult to follow. If this is the case, cut a hole in one of the smaller branches, take a fine blow-pipe and direct a current of air on the vein until it strikes the aperture and distends it so that it is readily seen, then insert the tip of the blow-pipe, and inflate the veins with air. Repeat this successively during the course of the dissection.

Dissection of the Arteries.—Clear away the connective tissue around the large vessels at the base of the heart, extend the neck, and remove the skin on

the latero-ventral surfaces. Trace the anterior arteries. (Pls. 24, 31, 33; Pl. 32, fig. 1). Follow the arteries round (Pl. 33). Trace the posterior veins and arteries (Pl. 27, fig. 1; Pl. 28, figs. 1 and 2; Pls. 29, 33, 34, 35).

Arteries and Veins of the Carapace.—These are best seen in specimens in which the horny shields have been removed and the bony plates decalcified, as described in the text. The details will, however, only be well seen in injected specimens (Pl. 28, fig. 1).

The Reno-reproductive Organs (*Pl. 36, fig. 3; Pl. 37, fig. 2; Pl. 38, figs. 1, 2*).

Divide the pelvic bones along the medio-ventral line, and force the halves apart, then separate the underlying muscles. Clean the ventral wall of the cloaca back to its external aperture. Pass a pair of forceps through the aperture and dilate the chamber by spreading the forceps apart. Slit the cloaca along one side and the urinogenital sinus anterior to it.

Dissection of the Heart.—Ligature the anterior arteries and veins a short distance from the heart, and cut through the vessels external to this, remove the heart and preserve it for future dissection (Pl. 31, figs. 1, 2; Pl. 32, fig. 1).

Respiratory Organs.—Inflate the lungs from the glottis, and examine the air passages and lungs.

The Nervous System.—The Spinal Nerves are best followed in a specimen in which the carapace has been decalcified. (Pl. 39.) The figures will supply a practical guide on other points.

The author of this Memoir is only responsible for the dissections, descriptions, and the supervision of the drawings. He has, therefore, to express his great indebtedness to several of his former students at Manchester University, more especially to Miss Maud Jepson, M.Sc., Miss E. A. Taylor, M.Sc., Miss Ruth Charlesworth, B.Sc., and to the professional artist, Miss Elwyn Bacon. He is also indebted to L. H. Hyman and the University of Chicago Press for permission to use fig. 2, Pl. 36; similarly to Professor E. S. Goodrich for fig. 1, Pl. 36, and to Messrs. Macmillan & Co. for fig. 5, Pl. 32.

EXPLANATION OF PLATES.

PLATE 19.

FIG.

1. Diagram of the dorsal surface of the carapace showing the position of the shields. The names of the shields are as indicated in the figure.
2. Diagram of the ventral surface of the plastron to show the position of the horny epidermic shields. The names of the shields are as indicated.

FIG.

3. Diagram of the dorsal surface of the carapace indicating the relative positions of the external horny shields and the more internal bony plates. The outlines of the shields are in even black lines, those of the plates are dotted. The names of the shields and plates may be taken from figs. 1 and 4.
4. Diagram of the dorsal surface of the carapace after removal of the shields, showing the bony plates. The names of the plates are as indicated in the figure.
5. Diagram of the internal surface of the carapace with the pectoral and pelvic girdle in position. The ten centra of the dorsal vertebrae are indicated and the ten ribs. The outlines of the bony plates are dotted, those of the horny shields are in even black lines. Ribs numbered, 1–6 and 10.
6. Diagram of an oblique dorsal view of the internal surface of the plastron showing the bony plates, and the hyoplastral and hypoplastral bridges connecting the plastron with the carapace.

Figures 1–6 were drawn by Miss M. Jepson.

7 and 8. Photographs from the dorsal and ventral surfaces respectively of a *Testudo ibera* six weeks after hatching. The specimen was one of several hatched, and reared for a few weeks in England (a very rare occurrence). A "Talk" on the hatching and rearing of these specimens was given by Mrs. M. H. Drake of Dulwich at the B.B.C. Studio in January, 1927.

PLATE 20.

1. Posterior surface of the skull of Testudo. Occ. cr. = occipital crest; Sup. occ. = supraoccipital; Par. = parietal; Temp. fos. = temporal fossa; Pt. fr. = postfrontal; Qu. jug. = quadrato-jugal; Squam. = squamosal; Quad. = quadrate; Occ. cond. (B.O.) = occipital condyle (basioccipital); Bas. occ. = basioccipital; Ex. occ. = exoccipital; Foram. = nerve foramina; Tymp. rec. = tympanic recess; Opisth. = opisthotic; For. mag. = foramen magnum.
2. Dorsal surface of the skull of Testudo. Premax. = premaxilla; Prefront. = prefrontal; Front. = frontal; Max. = maxilla; Ant. pt. of T.F. = anterior part of temporal fossa; Lat. bo. = lateral bone; Par. = parietal; Temp. fo. = temporal fossa; Tym. rec. = tympanic cavity; Sup. occ. = supraoccipital; Occ. cr. = occipital crest; Ex-occ. = exoccipital; Opisth. = opisthotic; Squam. = squamosal; Art. pt. qu. = articular part of quadrate; Proot. = prootic; Qu-ju. = quadrato-jugal; Po. fr. = post-frontal; Jug. = jugal; Max. = maxilla.
3. Internal surface of upper horny jaw.
4. Internal surface of lower horny jaw.

FIG.

5. External surface of one side of upper horny jaw. Post. = posterior end.
6. External surface of lower horny jaw. Post. = posterior end.
7. External surface of lower jaw. Artic. = articular; Sup.-ang. = supra-angular; Coron. = coronoid; Comp. = complementare; Dent. = dentary.
8. Internal surface of half of the lower jaw; the same lettering as above and Oper. = opercular.
9. Lateral view of atlas vertebra. Cen. = centrum; Arch. = neural arch; Fo. = fossa for spinal cord; Post zyg. = post zygapophysis; Ant. = anterior end.
10. Lateral view of axis vertebra. Odont. proc. = odontoid process; Lat. pr. = lateral process; Art. proc. = articular process; Ne. sp. = neural spine; Po. art. su. = posterior articular suture; Ce. = centrum; Hypap. = hypapophysys; Post zyg. = post zygapophysis.
11. Lateral view of third cervical vertebra. Ce. = centrum; Hyp. = hypapophysis; Lt. pr. = lateral process; Pr. zyg. = pre-zygapophysis; Po. zyg. = post-zygapophysis.

Drawings by Miss E. A. Taylor.

PLATE 21.

1. Lateral surface of skull. Occ. cr. = occipital crest; Su. oc. = supra-occipital; Par. = parietal; Qu. ju. = quadrate-jugal; Po. fr. = postfrontal; Fr. = frontal; Pr. fr. = prefrontal; Max. = maxilla; Orb. = orbit; P. mx. = premaxilla; Pal. = palatine; Jug. = jugal; Pal. Mx. = palatine and maxilla; Tem. fo. = temporal fossa; Pt. pr. ba. & pt. = pterygoid process of basisphenoid and pterygoid; Qu. = quadrate; Ex. occ. = exoccipital and paroccipital process; Occ. con. = occipital condyle; Ty. ca. = tympanic cavity; Sq. = squamosal.
2. Ventral surface of Skull. Ba. sp. = basisphenoid; Pal. fo. = palatal foramen; Vom. = vomer; Ba. occ. = basioccipital; other lettering as in previous figures of skull.
3. Lateral view of seventh cervical vertebra. Pr. zyg. = pre-zygapophysis; Ru. ne. sp. = rudimentary neural spine; Po. zyg. = post-zygapophysis; Ne. ar. = neural arch; Po. art. = posterior articular surface of centrum; Sut. = suture between centrum and neural arch; Hyp. = hypapophysis; Lt. pr. = lateral process; Pr. zyg. = pre-zygapophysis.
4. Lateral view of eight cervical vertebra. Same lettering as above.
5. Caudal vertebra from the ventral surface. Tr. pr. = transverse process; Ce. = centrum; Po. zyg. = post-zygapophysis; Bic. ar. = biconvex articulation of centrum; Ant. co. ar. = anterior convex articulation of centrum.
6. Atlas vertebra, anterior view of. Ar. pr. = articular process; Inc. ar. = incomplete arch; Ne. ca. = neural canal; Lig. tr. = ligamentum transversum; Lt. pr. = lateral process; Cav. = cavity for odontoid process

Drawings by Miss E. A. Taylor.

PLATE 22.

FIG.

1. Ventral and posterior view of the atlas vertebra. Tr. li. = transverse ligament; Cav. = cavity for odontoid process; Cen. = centrum; Lat. pr. = lateral process; Art. sur. = artic. surface (see other figs.).
2. Ventral view of axis vertebra. Od. pr. = odontoid process; Pr. zyg. = pre-zygapophysis; Hyp. = hypapophysis; Cen. = centrum; For. = notch for third spinal nerve; Po. zyg. = post-zygapophysis; Po. co. su. = posterior concave surface.
3. Ventral view of third cervical vertebra. Ant. conv. cen. = anterior convex articulation of centrum; Po. conc. ce. = posterior concave surface; other lettering as previously.
4. Ventral view of fourth cervical vertebra. Lettering as previously.
5. Ventral view of fifth cervical vertebra. Ant. bic. ce. = anterior bi-concave surface of centrum; Pos. bic. ce. = posterior biconvex surface of centrum; other lettering as for fig. 2.
6. Ventral view of sixth cervical vertebra. Ant. bic. ce. = anterior biconcave surface of centrum; Pos. bic. ce. = posterior biconvex surface of centrum; other lettering as for fig. 2.
7. Ventral view of seventh cervical vertebra. Ant. bic. ce. = anterior bi-concave surface of centrum; Pos. bic. ce. = posterior biconcave surface of centrum; other lettering as for fig. 2.
8. Ventral view of eighth cervical vertebra. Ant. art. ce. = anterior articular surface of centrum; Pos. co. ce. = posterior convex surface of centrum; Sh. ce. = short centrum; other lettering as for fig. 2.
9. Skeleton of the left posterior limb; Tr. mi. = trochanter minor; Hd. = head of femur; Tr. ma. = trochanter major; Fe. = femur; Co. = condyles of femur; Ru. sul. int. = rud. sulcus internus; Ti = tibia; Fi = fibula; Tib. + int. = tibiale + intermedium; Fib. = fibulare; Dis. ta. = distal tarsals; Met. = metatarsals; Ph. = phalanges, Digs. 1–4.

Drawings by Miss E. A. Taylor.

PLATE 23.

1. Ventral view of pelvic girdle, the cartilaginous portion is dotted. Pu. = pubis; La. pu. pr. = lateral pubic process; Ob. fo. = obturator foramen; Acet. = acetabulum lined by cartilage; Il. = ilium which proceeds in a dorsal direction; Isch. = ischium.
2. Left Anterior limb. Head = head of humerus; Art. sul. = articular sulcus; Md. pr. = medial process (tuberculum externum of Bojanus); Lt. pr. = lateral process (tuberculum internum of Bojanus); Hu. = humerus; Ext. con. tub. = external condylar tubercle; Ol. pr. = olecranon process;

Ul. = ulna; Ra. = radius; Uln. = ulnare; Cen. = centrale; Rad. = radiale; Int. = intermedium; 1st, 2nd, 5th dis. car. = distal carpals; R. met. = row of metacarpals; Dig. 1, Dig. V = digits I and V.

Drawings by Miss E. A. Taylor.

PLATE 24.

Viscera of female Testudo in situ. Note:—L. ao. = left aortic arch; Pul. ar. = pulmonary artery; L.A. = left auricle; Per. = pericardium; Per. m. = pericardial membrane; L.V. = left side of the ventricle; L. li. = left lobe of the liver; T. li. = transverse lobe of the liver; St. = stomach; Sm. In. = part of the small intestine; Ov. = oviduct; Pu. = position of the pubes; Mar. sh. = marginal shields; Isch. = position of the ischium; Ta. = tail; Ova; R. li. = right lobe of the liver; R.V. right side of ventricle; Par. per. = parietal peritoneum; R.A. = right auricle; Cor. = position of the coracoid; In. art. = innominate artery.

Drawing by Miss M. Jepson.

PLATE 25.

Dissection of a Female Testudo, to expose the alimentary canal and the viscera. The lobes of the liver have been lifted, and turned anteriorly. The intestine has been unravelled to show the sequence of its course. The names of the parts are indicated on the plate.

Drawing by Miss M. Jepson.

PLATE 26.

FIG.

1. The liver and adjoining parts; the liver has been turned anteriorly, so as to expose the posterior surface. R. li. lo. = right lobe of liver; Lat. = lateral part of last; Ga. bl. = gall bladder; Med. = median lobe of liver; Bd. vess. = blood vessels; Med. isth. = median isthmus or neck of liver with anterior and posterior portions; Par. per. = parietal peritoneum; L. li. lo. = left lobe of liver; Cd. stom. = cardiac part of stomach; Dor. l. li. lo. = dorsal extension of the left lobe of the liver, which is surrounded by the cardiac part of the stomach; Pyl. stom. = pyloric part of stomach; Liv. = liver; Pyl. = pylorus; Mes. = mesentery; Duod. = duodenum; Cl. = cleft.
2. Diagram of anterior abdominal veins entering liver and of the anterior part of the hepato-portal system, from the ventral surface (partly after Bojanus). R. ant. ve. ca. = opening of right anterior vena cava into sinus venosus; Sin. ven. = sinus venosus; L. ant. ve. ca. = opening of left anterior vena cava into sinus venosus; Port. = portal veins leading

FIG.

into main transverse portal vein; L. ant. abd. = left anterior abdominal; R. ant. abd. = right anterior abdominal; Pos. ve. ca. = posterior vena cava; Hep. = hepatic veins; Ap. = aperture into right auricle; Liv. = liver indicated by dotted lines.

3. Diagram to show the more ventral veins which pass from a lateral position in a medial direction to join the transverse pelvic vein from which the two anterior abdominals pass anteriorly; Epig. = to epigastric; Lat. = lateral; Car. = carapaxal; Pel. = superficial pelvic; Dor. br. = dorsal branch.

Drawings by Miss M. Jepson.

PLATE 27.

1. Diagram of anterior abdominal and posterior veins of injected specimen from the ventral surface. The heart and anterior arteries from another specimen are placed in position. The pectoral muscles, liver and kidneys, etc., are indicated by dotted lines. Pect. ve. = pectoral veins; Brach. ve. = brachial veins; Pect. mus. = pectoral muscles, + indicating where a connection takes place with the intercostal; L. hep. port. ve. = left hepatic portal vein to the left lobe of the liver, a corresponding one on the right; Liv. = liver; Ven. sup. br. = small superficial branch from ventral wall and plastron; Tr. pub. ve. = transverse vein on surface of pubic region which connects with the two anterior abdominals; Sup. car. ve. = superficial branch veins from carapace at another level from those behind; La. br. com. il. = large branch of common iliac; Sm. br. com. il. = small branch of common iliac or external renal portal; Com. il. ve. = common iliac vein; Pos. car. ve. = posterior veins of carapace leading into common iliac; Fem. & Sc. = femoral and sciatic veins; Sup. pel. ve. = superficial pelvic veins; ++ = second bridge formed by the superficial pelvic veins connected anteriorly with the anterior abdominals; L. ant. abd. = left anterior abdominal; Rt. ant. abd. = right anterior abdominal; Vent. = ventricle.
2. Diagram of anterior veins partly from ventral surface. Pt. ve. ca. = posterior vena cava; Pul. art. = pulmonary artery; R. ant. ve. ca. = right anterior vena cava; L. sys. = left systemic artery; In. = innominate artery; R. pul. ve. = right pulmonary vein; R. scap.. = right scapular vein; R. sb. cl. = right subclavian vein; R. br. = right brachial vein; R. ex. jug. = right external jugular vein; R.V. = right side of ventricle; L.V. = left side of ventricle; Sin. ven. = sinus venosus with opening into right auricle; L. thyr. = left thyroideal with thyroid gland median to it; L. Scap. = left scapular vein; L. oes. = left oesophageal vein.

FIG.

3. Right anterior vena cava injected and dissected from the side. R. ant. ve. cav. = right anterior vena cava; R. aur. = right auricle, part of; Thyr. = thyroideal vein; Sc. = scapular vein; Oes. = oesophageal vein (Bojanus), int. jugular (Hyman); S. cl. = subclavian; C. vert. = common vertebral (Bojanus), external jugular (Hyman); Cervs. = cervicals; × = connection with common azygous; + = connection with anterior transverse intercostal; Ex. jug. = external jugular (jugular, Bojanus); Br. n. & h. = branches from head and neck; Anas. = anastomosis; Pec. g. & m. = pectoral girdle and muscles; Br. = brachial.
4. Crossing of Azygous veins. Azy. = Azygous veins; Con. ve. = connecting vein (see text and other fig.).

Figure 1 drawn by Miss Elwyn Bacon, figures 2, 3, 4 are by Miss Ruth Charlesworth.

PLATE 28.

1. Arteries and veins on the dorsal surface of the animal injected, and the carapace removed. Note the following:—Anastomosis with jugular vein; Connection with external jugular; + Branch passes to connect with anterior abdominal; Anastomosing vessel formed by union of the transverse intercostal veins; Transverse intercostal vein; Right azygous or common descending intercostal vein; Costal artery and vein; Dorsal vertebral veins; Right spinal artery; × = branch to kidney; Anterior renal portal; To connection with the commencement of the anterior abdominal; Common posterior or recurrent intercostal artery and vein; Branch to common iliac artery and vein; Mus. = muscles; Branches of iliac artery and vein; Branch to common iliac artery; Epigastric vein; Left spinal artery; Epigastric artery and vein; Anastomosing vessels formed by the transverse intercostal arteries and veins; Dorsal part of neural arch; Com. desc. interc. art. = common descending intercostal artery; as a whole, the strength of these arteries and veins is exaggerated in the figure.
2. Right and left anterior abdominal veins and their branches (in ♂ specimen) to illustrate the great variation which occurs in the distribution of those veins. Liver and heart dotted; Pect. mus. = pectoral muscles; Liv. = liver; L. ant. abd. = left anterior abdominal; Br. l. = branch from liver; Car. = branch from carapace; Br. th. = branch from ventral surface of thigh; Sup. pel. = superficial pelvics; Pos. tr. pub. ve. = posterior transverse pubic veins; Tr. pub. ve. = transverse pubic veins; R. ant. abd. = right anterior abdominal, not connected with superficial pelvics posteriorly; Pec. & brach. = pectoral and brachial branches; Ht. = heart; Plas. mem. = membrane connecting with plastron.

Fig.

3. Renal veins and posterior vena cava from injected specimen ♀, dissected from the ventral surface. Gen. = genitals; Ren. plex. = renal plexus; Pos. ve. ca. = posterior vena cava; Hep. = hepatic veins; Liv. = liver; R. aur. = right auricle.
4. Branches of the common carotid artery. Ling. = lingual artery; C. car. = common carotid artery.

Fig. 1 by Miss Bacon, figs. 2, 3, 4 by Miss Charlesworth.

Plate 29.

1. Diagram of renal portal veins. Note the following:—Posterior vena cava; Left renals; Posterior renal portal; Genital veins; Vesicular veins; Hæmorrhoidal veins; Rectal veins; Left anterior abdominal vein; Transverse pelvic bridge; Superficial pelvic vein; Crural vein; Left gonad; Left kidney; ventral surface; Anterior renal portal vein; × = connection with azygous vein; External renal portal; Common azygous vein; Transverse intercostal; Rami communicates between veins of carapace and posterior and external renal portals; C. anas. = common anastomosing longitudinal vein formed from the transverse intercostals; Carapace = ventral surface of carapace with veins as shown in other fig. Veins from posterior part of carapace and tail; Common iliac vein; Bifurcation of common iliac into transverse pelvic and external renal portal veins; Femoral and sciatic veins; Anastomosis of dorsal pelvic muscles. N.B.—The veins dotted are at an entirely different level from the others, they come from underneath the dorsal surface of the carapace. The superficial and lateral veins and more ventral veins joining the lateral part of the transverse pelvic bridge shown in another figure are not given in this figure.
2. Diagram of the arteries lying underneath the carapace. Car. = carapace; Com. des. int. = common descending intercostal artery; Cerv. art. = cervical artery; Co. int. mamm. = connection with internal mammary artery of Bojanus; Com. ver. = common vertebral artery; Scap. = scapular arteries; Subcl. = subclavian artery; In. = innominate artery; Asc. ar. = ascending axillary artery; Des. ax. = descending axillary artery; Brach. = brachial artery; Int. circ. hum. = internal circumflex humeral; Ext. circ. hum. = external circumflex humeral; Thor. = thoracic artery; Int. Mam. = internal mammary of Bojanus; Epig. = epigastric artery; Ar. le. = artery from leg; Cl. art. from cloaca, etc., Dors. aor. = dorsal aorta; Con. com. des. int. = connection with common descending intercostal; Tr. interc. = transverse intercostal artery.

Figure 1 by Miss E. A. Taylor, figure 2 by Miss Charlesworth.

PLATE 30.

Diagram showing the biliary and hepatic ducts. Ga. bl. = gall-bladder embedded in the right lobe of the liver; Cys. = cystic duct; R. l. liv. = right lobe of liver; Hep. du. = hepatic ducts; Anas. hep. du. = anastomosis of hepatic ducts; Pancr. = pancreas; Duod. = duodenum; Com. sm. int. = commencement of small intestine; Panc. du. = pancreatic ducts; Op. chol. du. = opening of choledochic duct into duodenum; Op. cyst. du. = opening of cystic duct into duodenum.

Drawing by Miss M. Jepson.

PLATE 31.

FIG.

1. The heart and anterior arteries (injected) exposed and drawn from the ventral surface. They do not agree exactly with those of *Emys nigricans*. In the drawing the space between the forking of the innominate and the giving off of the common carotid is slightly too long. The nature of the blood is indicated. The heart has been pulled backwards, and the parts stretched. Note:—Right side of ventricle; Right auricle; Right branch of common pulmonary; Right aortic arch; Right subclavian artery; Right common carotid; Right oesophageal artery; Thyroid gland and thyroideal arteries; Left oesophageal; Left common carotid artery; Left subclavian artery; Innominate artery; Left aortic arch; Left auricle; Common pulmonary artery; Left side of ventricle.
2. Anterior arteries drawn from the right side (of the animal) and the auricles and ventricle turned upwards and towards the left. R. aur. = right auricle; L. aur. = left auricle; Ventr. = ventricle; Art. tr. = arterial trunks coming off from the ventricle; Innom. art. = innominate artery; R. subcl. art. = right subclavian artery; R. com. car. art. = right common carotid artery; R. aor. ar. = right aortic arch; R. pul. art. = right pulmonary artery.
3. Diagram of branches of left subclavian artery from an injected specimen (for relation to other parts, see other figure). L. subcl. = left subclavian artery; Des. ax. = descending axillary; Int. circ. hum. = internal circumflex humeral; Ext. circ. hum. = external circumflex humeral; Pl. ep. = plexus with epigastric; Thor. = thoracic; Ep. art. = epigastric artery near vein; Asc. ax. = ascending axillary; Brach. = brachial; Dors. br. brach. = dorsal branch of the brachial and small branch to the fore-limb (unnamed) beneath it; Com. vert. = common vertebral; Scaps. = scapular arteries; C. anas. br. = branch to common anastomosing branch of the transverse intercostals (internal mammary of Bojanus); Br. com. des. interc. = branch to common descending intercostal, near vertebral column.
4. Diagram of anterior arteries from the side. The subclavians are at first ventral to the carotids; In. = innominate artery; R. scl. = right

Fig.

subclavian artery; L. scl. = left subclavian artery; L. Aor. = left aorta; C. pul. = common pulmonary artery; Oes. = oesophageal artery; C. car. = common carotid; I.c.h. = internal circumflex humeral; E.c.h. = External circumflex humeral; Th. = thoracic; P. mus. = pectoral muscles; Asc. ax. = ascending axillary; C. v. = common vertebral; Anas. = anastomosis; Br. = brachial; C. des int. = common descending intercostal; Int. mam. = internal mammary (Bojanus); V. = origin of common vertebral, etc.

5. Bifurcation into the innominate arteries from the common trunk. In. = innominate; L. subcl. = left subclavian; Th. gl. = thyroid gland; L. oes. = left oesophageal; L. c. car. = left common carotid.

Figs. 1, 2, 4 by Miss E. Bacon, figs. 3 and 5 by Miss M. Jepson.

Plate 32.

1. Anterior arteries (injected) passing from the ventricle, viewed from behind, the heart having been turned anteriorly. R. aur. = right auricle; L. aur. = left auricle; Ventr. = ventricle; Innom. art. = innominate artery emerges from the left side of the ventricle); Com. pul. art. = common pulmonary artery, arises from the right side of the ventricle; L. pulm. art. = left pulmonary artery; R. pulm. art. = right pulmonary artery; R. aort. arch = right aortic arch; R. Subcl. art. = right subclavian artery.
2. Generalised diagram of the veins from the leg and tail. Car. = carapace; Com. il. = common iliac; Sciat. = sciatic; Fem. = femoral; Crur. = crural; Abdominal (anterior) abdominal; S. pel. = superficial pelvics; Plas. = plastron; Circ. il. = circumflex iliac; Ta. = tail; Cocc. = coccygeal vein; L. = leg.
3. Posterior arteries, some of the, dissected from the left side dorsally. Dors. aor. = dorsal aorta; R. com. il. = right common iliac artery; R. hyp. art. = right hypogastric artery; L. hyp. art. = left hypogastric artery; Epig. = epigastric artery; Cr. = crural of femoral artery; Vent. br. c. il. = ventral branch of common iliac artery; Inf. cocc. = inferior coccygeal or median sacral artery; Il. = ilium; Pel. mus. = pelvic muscles; Sciat. = sciatic artery; Pud. art. = pudic artery cut short; Ve. = veins cross-hatched lying ventral to the arteries; B. = probably femoral vein.
4. Diagram of superficial appearance of the lungs.
5. Diagrammatic transverse section through the shell of Testudo, partly after Gadow, "Amphibia and Reptiles," Cambridge Natural History, p. 323, fig. 68 A. N. p. = neural plate; C. sh. = costal shield; C. pl. = costal plate; Mar. pl. = marginal plate; Pl. = plastron; Vert. = vertebra; Cap. = capitulum of rib; Sp. c. = spinal cord; the shields are shown in black, the plates dotted.

FIG.

6. Buccal cavity widely opened; the junctions of the upper and lower jaws having been severed. Ext. na. = external nares; H. upp. jaw = horny upper jaw; Ext. sur. jaw = external surface of jaw; Pas. oes. = passage to oesophagus; Int. na. = internal nares; L. jaw c. = lower jaw cut; Eus. ap. = Eustachian aperture; Gl. = glottis; Mus. cut. = muscles cut; Tg. = tongue; H. lo. j. = horny lower jaw; Musc. = muscles.

Figs. 1, 2, 3 by Miss E. Bacon, figs. 4, 5, 6 by Miss M. Jepson.

PLATE 33.

General diagram of the arterial system. In. = innominate artery; R. aor. = right aortic arch; Thyr. = thyroideals; Oes. = oesophageal; Car. = carotid; Pul. = pulmonary artery; L. aor. = left aortic arch; Des. ax. = descending axillary branch of the subclavian artery; Int. c. h. = internal circumflex humeral; Ex. c. h. = external circumflex humeral; Thor. = thoracic; Plex. = plexus between the last vessels and the epigastric; Epig. = epigastric; Asc. ax. = ascending axillary branch of the subclavian artery; Sc. = scapulars; C. v. = common vertebral; Brach. = brachial; D. br. = dorsal branch of the brachial; C. des. int. cont. = continuation of ascending axillary to connect with the common descending intercostal; Card. = cardiac; Coel. & mes. = coeliac and mesenteric arteries (compare other fig.); Con. br. epig. = connecting branches between the epigastric and common anastomosing intercostal; Par. = parietals; Ren. g. = reno-genital; Gen. = genital; Ren. art. = reno-uterine arteries and posterior to them, the common iliacs; Com. des. int. = common descending intercostal; C. a. br. = common anastomosing branch of the transverse intercostals; L. ca. = lateral caudal; V. br. = ventral branch of the common iliac; Fem. = femoral; Hyp. = hypogastric; Sciat. = sciatic; Sac. v. = sacral art.; Pud. = pudic; Haem. = haemorrhoidal; Pel. = pelvic; Dorsal aorta in the median line, and common iliacs at bifurcation.

Drawing by Miss E. A. Taylor.

PLATE 34.

Diagram of the venous system generalised from the detailed figures as dissected. R. subcl. = right subclavian vein; Pul. ve. = pulmonary vein; R. oes. = right oesophageal; L. int. jug. = left internal jugular; L. brach. = left brachial; R. ext. jug. = right external jugular; L. thyr. = left thyroideal; Two main anterior veins on either side = the right and left anterior venae cavae leading into the sinus venosus; Hep. = hepatic veins passing into sinus venosus; Pect. = pectoral veins, communicating with anterior end of anterior abdominals; Port. = portal veins from

alimentary canal leading into main transverse portal vein beneath the liver; R. ant. abdom. = right anterior abdominal, running parallel with the left anterior abdominal; Pos. ve. ca. = posterior vena cava; Gon. = gonad ♂; Liv. = liver; Kid. = kidney; Po. re. p. = posterior renal portal; Eff. ren. = efferent renal veins; Az. = azygous vein; R. c. = Rami communicantes; Com. il. = common iliac; Sup. pel. = superficial pelvic; Fem. = femoral; Sci. = sciatic; Car. = carapaxal; Sup. ve. = superficial veins from carapace; Po. re. p. = posterior renal portal; Ext. ren. port. = external renal portal; Ant. ren. por. = anterior renal portal; Gen. = genitals; R. c. = right carapaxal veins; Sup. ve. = superficial veins; R. = right innominate artery; L. = left innominate artery. Drawing by Miss E. A. Taylor.

Plate 35.

Part of the arterial system from the dorsal surface, injected and the lungs removed. Female specimen. L. aor. ar. = left aortic arch; L. card. = left cardiac; Gast. = gastric; Oes. = Oesophagus; R. aor. ar. = right aortic arch; Liv. = liver; L. int. = large intestine; Coel. = coeliac; Dors. aor. = dorsal aorta; P. m. = posterior mesenteric; Par. = parietals, three pairs; Spl. duod. = spleno-duodenal; Mes. = mesenteric; Ant. mes. = anterior mesenteric; Duod. = duodenum; St. = stom.; Duod. art. = duodenal artery; Il. col. = ileo-colical; Post. ve. ca. = posterior vena cava; Mes. = mesentery; Sm. int. = small intestine; Spl. = spleen; Re. gen. = reno-genital; Kid. = kidney; Com. il. = common iliac; Rec. inte. = recurrent intercostal artery; V. br. = ventral branch of common iliac; Epig. = epigastric; Ren. = renals (three pairs); Pel. gir. = pelvic girdle; Cr. = crural or femoral; Hyp. = hypogastric; Sciat. = sciatic; Pud. = pudic; Saer. = sacral or inferior coccygeal. Drawing by Miss M. Jepson.

Plate 36.

Fig.

1. The arterial arches after Goodrich "On the Classification of the Reptilia." The heart is represented as untwisted so as to bring the chambers into a single plane, with the sinus venosus behind and the ventricle in front. T. = transverse section through the truncus arteriosus; B. = transverse section through the region of the bulbis cordis; Ext. car. = external carotid; Int. car. = internal carotid; R. syst. ar. = right systemic arch; L. syst. ar. = left systemic arch; Pul. = pulmonary artery; Int. ven. sep. = interventricular septum; Int. aur. sep. = interauricular septum; Anterior venae cavae and posterior vena cava entering the reduced sinus venosus; 1–6, the arterial arches.

FIG.

2. Diagram taken from Hyman, 1922, by kind permission of the University of Chicago Press, to illustrate the divisions of the coelom in the turtle. The transverse septum and its derivatives are indicated by thick lines. In fishes, the coelom is divided into the pericardial cavity and the pleuroperitoneal cavity by the transverse septum; in Urodeles, the condition is similar to that of fishes, with, however, the addition of the lung which projects into the pleuroperitoneal cavity, in the turtle, "the pericardial cavity has descended posteriorly until it lies ventral to the anterior part of the pleuroperitoneal cavity, the anterior face of the transverse septum has now become part of the wall of the paricardial sac." The lung "is in contact with the inner surface of the carapace, and the parietal peritoneum passes over its ventral surface, leaving the lung outside of the membrane." Such a condition is termed *retroperitoneal.* The posterior end of the lung projects into the pleuroperitoneal cavity and is clothed with the peritoneum. Lg. = lung; Par. per. = parietal pericardium or pericardial sac; Pl. per. cav. = pleuroperitoneal cavity; Liv. = liver; Cor. lig. = coronary ligament; Tr. sep. = transverse septum.
3. Surface of the kidney, part of the; showing the resemblance to cerebral gyri or convolutions; blood-vessels run in the centre of the lobelets. Part of an original drawing by Miss M. Jepson.

PLATE 37.

1. Anterior arteries dissected from the left side; the right aorta is concealed from view of the other vessels. R. br. = right bronchus; Thyr. = thyroid gland; In. = innominate artery; Ven. = ventricle; L. aur. = left auricle; L. com. pul. = left branch of common pulmonary artery; Pec. mus. = reflected muscles of pectoral girdle; Oes. art. = oesophageal artery; Int. circ. hum. = internal circumflex humeral; Ext. circ. hum. = external circumflex humeral; Thor. = thoracic artery; L. subcl. = left subclavian artery; L. com. car. = left common carotid; L. syst. ar. = left aortic arch; Vert. = vertebral or common cervical; Brach. = brachial; Anas. = anastomosing branch; C. des. int. = common descending intercostal; F. int. = first intercostal to internal mammary; L. aor. ar. = left aortic arch.
2. Anterior view of the male urinogenital organs, the right testis has been removed and the bladder turned posteriorly. Rect. = cavity of the rectum which has been cut transversely; L. tes. = left testis; L. kid. = left kidney; V. ef. = vasa efferentia; Epid. = epididymis; M. d. = left Müllerian duct; Ur. = left ureter; L. v. de. = left vas deferens; Bl. = bladder; R. ur. = right ureter; R. kid. = right kidney; R. v. de. = right vas deferens; R. m. d. = right Müllerian duct; Per. = peritoneum

FIG.

investing epididymis; Mes. = mesentery; R. ad. = right adrenal body; R. kid. = right kidney; Dotted outline indicates the position of the right and left hind-limbs; Arrows indicate the bladder.

Drawings by Miss M. Jepson.

PLATE 38.

1. Female urinogenital organs from the ventral surface. Ov. = ovary; Rect. = rectum; R. kid. = right kidney; R. ur. = right ureter; R. aper. = aperture of the right ureter into urinogenital sinus; Pos. pt. ur. sin. = posterior part of urinogenital sinus; Cl. = cut wall of cloaca; Ta. = tail cut open; Bl. = bladder; Pt. bl. = part of the bladder opened showing the internal wall; Ed. bl. = cut edge of wall of bladder; L. ovi. = anterior end of left oviduct cut; L. ur. = left ureter cut; Ov. aper. = opening of left oviduct into the urinogenital sinus; Clit. = posterior part of clitoris. The terminus of the rectum or anus is situated more dorsally and is not shown in the drawing.
2. Male urinogenital system dissected from the ventral surface and drawn from the right side. The testis, rectum, and bladder have been lifted out of their natural positions. R. te. = right testis; R. epid. = right epididymis; Rect. = lumen of rectum, which has been cut transversely; V. d. & Ur. = vas deferens and ureter opening closely adjacent to one another into the urinogenital sinus; Bl.′ = neck of bladder; Bul. = bulbus; Cor. cav. = corpus cavernosa; Gl. pen. = glans penis; Cl. ap. = cloacal aperture; Cl. wa. = wall of cloaca; Ur. = ureter; Vas. def. = vas deferens; Müll. du. = Müllerian duct, or right rudimentary oviduct; Vas. eff. = vasa efferentia; R. kid. = right kidney; Per. = peritoneum investing epididymis.

Drawings by Miss M. Jepson.

PLATE 39.

Diagram of the spinal nervous system of Emys (partly after Bojanus). Letters and numbers :—3–9 = cervical nerves in succession; 3a = dorsal branch; 3 = ventral branch of third cervical nerve, and similarly in the other cases; 10–19 = dorsal spinal nerves; 12a = costal branch; 12 = subcostal branch and the others similarly; Rts. br. pl. 6, 7, 8, 9 = roots of the nerves which contribute to the brachial plexus; Nerves of brachial plexus only partially indicated; X = vagus nerve; Sc. = scapula; Mus. = cutaneous muscle; rad. = radial nerve; Uln. = ulnar nerve; Med. = medial nerve; R. c. = connecting ramus between spinal nerves, 10, 11, 12, 13; Sym. = sympathetic; 16a, 17, 18 = roots of sciatic plexus; Il. = ilium; Tib. = tibial nerve; Crur. = crural nerve; Isch. = ischiadic nerve; 19–21 = roots of ischiadic plexus. Drawing by Miss M. Jepson.

PLATE 40.

FIG.

1. Branches of the Trigeminal nerve, mainly after Bojanus. VA = ophthalmic branch; VA^3 = frontal branch of ophthalmic; VA^1 = ethmoidal branch of ophthalmic; VA* = branches of ethmoidal; VB = root of maxillary nerve; B^1 = zygomatic branch of; B^2 = lacrymal branch; B^3 = true lacrymal branches; B^4 = pterygoid branch; e = position of bony canal for vidian nerve; f = posterior nasal branches of vidian nerve; G = petrosal branch of vidian nerve; K = sympathetic branch of vidian nerve; B^5 = posterior palatine branch of maxillary; B^6 = anterior palatine branch of maxillary; B^7 = infra-orbital branch of maxillary; B^8 = true maxillary branch; VC = mandibular nerve; C^1 = temporal branch of; C^2 = buccal branch of; C^3 = other temporal branch of; C^4 = branch to pterygoid muscle; C^5 = alveolar branch of; C^6 = other alveolar branches; C^7 mylohyoid branch of. Note:—Nerve B^4 should be under C^2, C^3, C^4 *not* above as depicted in the figure.
2. Diagram of the 9th, 10th, 11th, and 12th cranial nerves of Emys and 2nd, 3rd, and 4th spinal nerves (after Bojanus). Numeral and lettering:— ix = glosso-pharyngeal; ix′ = branch of last anastomosing with laryngeal of x; ix″ = lingual of glossopharyngeal; x = root of vagus nerve; x lar. = laryngeal branch of vagus; x vag. = main trunk of vagus; Rec. vag. = Recurrent branch of x; Plex. = plexal branch of x; xi = spinal accessory, branch to sternomastoid muscle; xii = hypoglossal; xii ant. = anterior branch of hypoglossal; xii post. = posterior branch of hypoglossal; xii des. = descending branch of hypoglossal; Sy. = vidian nerve cut; Cer. sy. = cervical sympathetic continuation of last; 2, 3, 4 = second, third, and fourth cervical nerves and connections; In. cer. g. = inferior cervical ganglion; Med. cer. gn. = median cervical ganglion; L. aor. = left aorta; L. car. = left carotid; L. sub. ar. = left subclavian artery.

Drawings by Miss M. Jepson.

PLATES 41–43.

These three plates illustrate selected transverse sections of a series taken throughout the length of the body of a Testudo, six weeks old (see Pl. 19, fig. 7). The horny shields were firstly removed, and then the bony plates and internal bones gradually decalcified. The entire processes up to and including the embedding of the specimen in celloidin were carried through extremely slowly, extending over several months; the sections were cut with a Reichert sliding microtome. The sections were all drawn five to six times their actual size by Miss R. Charlesworth.

Plate 41.

Fig.

1. Transverse section of *Testudo ibera*, six weeks old, in the cervical region. Car. = carapace; Con. tis. = connective tissue; Lg. = lung; Integ. = integument; Ret. Neck = retractor muscles of neck; Cerv. Musc. = cervical muscles; Spin. co. = spinal cord; Cen. = centrum; F. l. = part of the fore-limb; Oes. = oesophagus; Tr. = part of trachea; Ven. mus. = ventral muscles; Plas. = plastron. Size of section, $\frac{11}{16}$ by $\frac{8}{16}$ of an inch.
2. Transverse section of *Testudo ibera* (six weeks old) slightly posterior to the last, after the bifurcation of the trachea into the two bronchi. Size of section, $\frac{7}{8}$ by $\frac{3}{8}$ of an inch. Car. = carapace; Con. tiss. = connective tissue; Lg. = lung; Cerv. mus. = dorsal cervical muscles; Liv. = liver; Ret. nk. = retractor muscles of neck; N. ar. = neural arch; Centr. = centrum; Fl. = parts of bones of fore-limb cut in various places; Mus. f. l. = muscles of fore-limb; Oes. = oesophagus; Bron. = bronchial tubes; Ven. Mus. = ventral muscles; Plas. = plastron.
3. Transverse section posterior to the last; lettering as previously and F. l. = anterior limb bones; Acrom. = acromial process of the scapula; C. = coelom. Size of section, $\frac{15}{16}$ by $\frac{9}{16}$ of an inch.

Plate 42.

1. Transverse section through the cardiac region. Stom. = stomach; Pec. mus. = pectoral muscles; Pec. g. = pectoral girdle; Sin. ven. = sinus venosus; Bd. v. = anterior arteries; Ht. = heart with indication of separation into chambers; the section is not equally orientated on both sides. Size of section, 1 in. by $\frac{15}{16}$.
2. Transverse section through intestinal region. Lettering as previously and in addition, Sp. ne. = spinal nerve; Int. = intestine cut at various places; Spl. = spleens; Port. ve. = portal vein; Mus. long. dors. = musculi longissimi dorsi. Size of section, $1\frac{8}{16}$ by $\frac{13}{16}$ of an inch.

Plate 43.

1. Transverse section in region of pelvic girdle and hind-limb bones. Kid. = part of the kidneys. Size of section, $\frac{7}{8}$ by $\frac{5}{8}$ of an inch.
2. Transverse section slightly posterior to the previous, note the pelvic girdle and muscles, the kidneys and bladder. Section same size as last.

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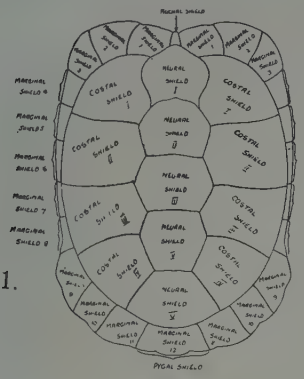
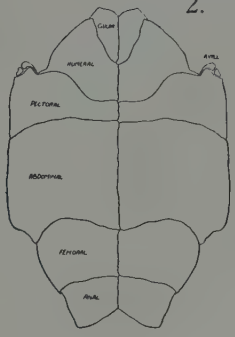
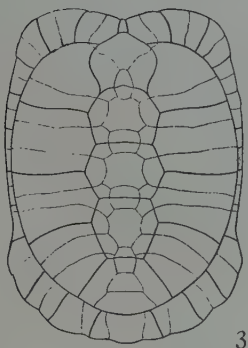

NUCHAL SHIELD
NEURAL SHIELD I
NEURAL SHIELD II
NEURAL SHIELD III
NEURAL SHIELD IV
NEURAL SHIELD V
COSTAL SHIELD I
COSTAL SHIELD II
COSTAL SHIELD III
COSTAL SHIELD IV
COSTAL SHIELD V
COSTAL SHIELD VI
COSTAL SHIELD VII
COSTAL SHIELD VIII
MARGINAL SHIELD 1
MARGINAL SHIELD 2
MARGINAL SHIELD 3
MARGINAL SHIELD 4
MARGINAL SHIELD 5
MARGINAL SHIELD 6
MARGINAL SHIELD 7
MARGINAL SHIELD 8
MARGINAL SHIELD 9
MARGINAL SHIELD 10
MARGINAL SHIELD 11
MARGINAL SHIELD 12
PYGAL SHIELD
1.


GULAR
HUMERAL
ANAL
PECTORAL
ABDOMINAL
FEMORAL
ANAL
2.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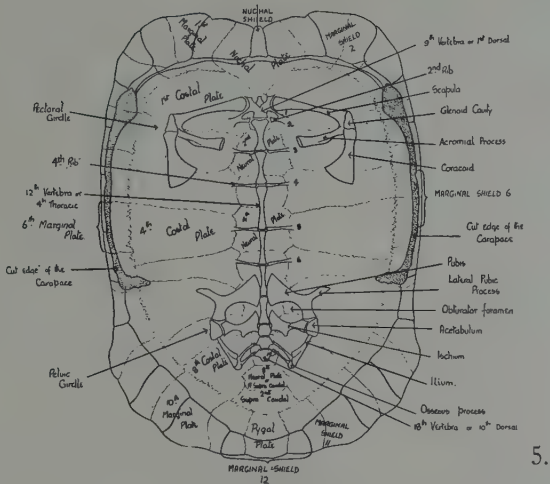
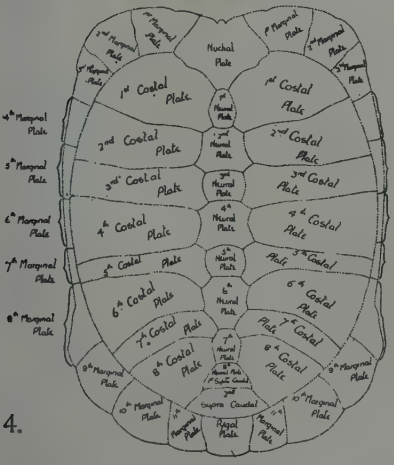
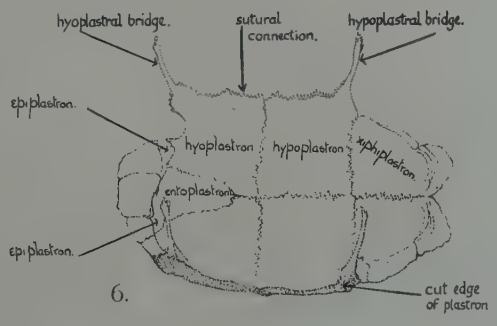
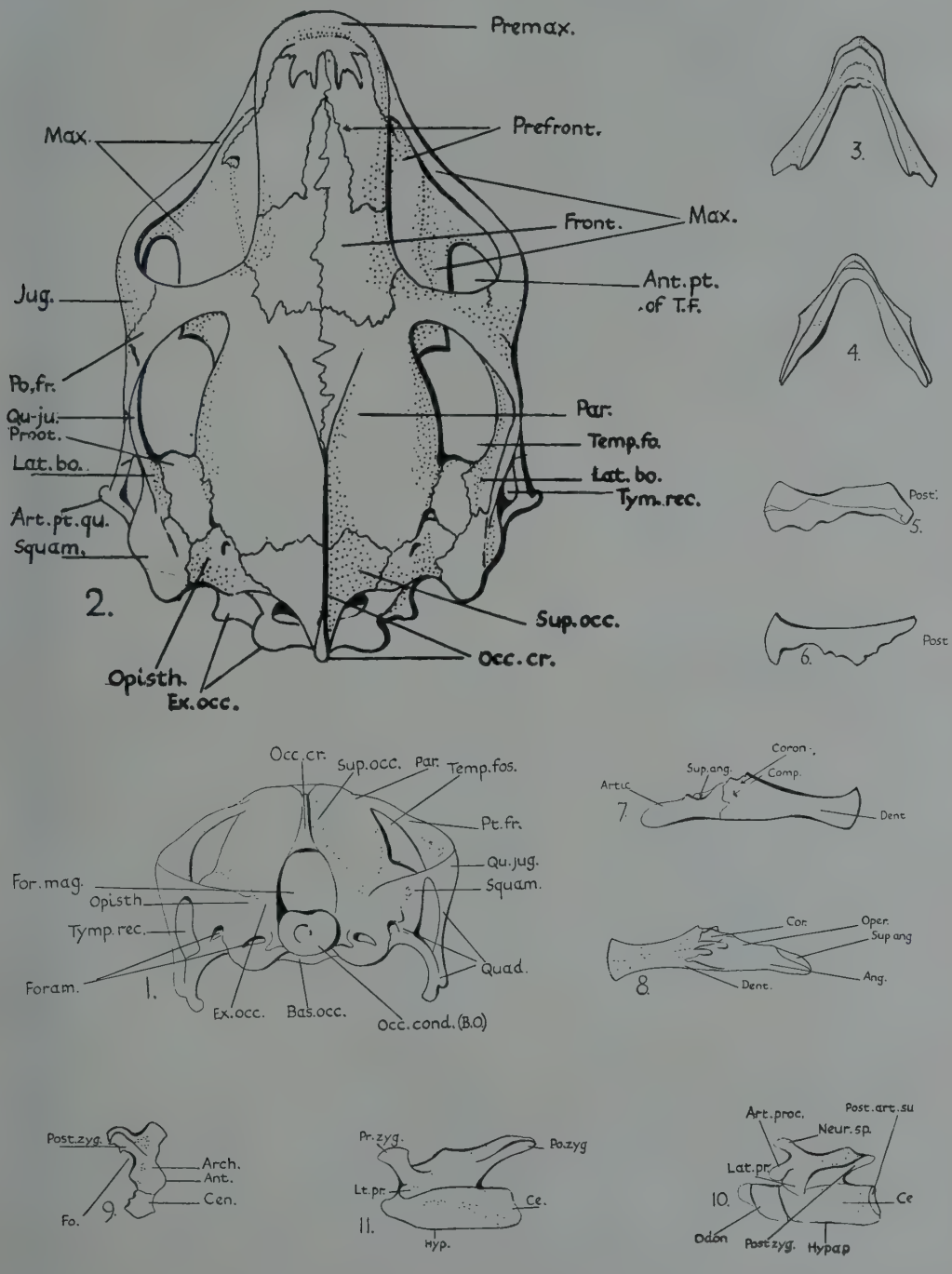

NUCHAL SHIELD
MARGINAL SHIELD 1
MARGINAL SHIELD 2
Nuchal Plate
1st Costal Plate
2nd Costal Plate
3rd Vertebra or 1st Dorsal
2nd Rib
Scapula
Glenoid Cavity
Acromial Process
Coracoid
Pectoral Girdle
4th Rib
12th Vertebra or 4th Thoracic
MARGINAL SHIELD 6
6th Marginal Plate
8th Costal Plate
Cut edge of the Carapace
Cut edge of the Carapace
Pubis
Lateral Pubic Process
Obturator foramen
Acetabulum
Ischium
Pelvic Girdle
Ilium.
9th Costal Plate
Supra Caudal
10th Marginal Plate
Obscure process
10th Vertebra or 10th Dorsal
Pygal Plate
MARGINAL SHIELD 11
MARGINAL SHIELD 12
5.


1st Marginal Plate
2nd Marginal Plate
3rd Marginal Plate
Nuchal Plate
1st Costal Plate
2nd Costal Plate
3rd Costal Plate
4th Costal Plate
5th Costal Plate
6th Costal Plate
7th Costal Plate
8th Costal Plate
4th Marginal Plate
5th Marginal Plate
6th Marginal Plate
7th Marginal Plate
8th Marginal Plate
9th Marginal Plate
10th Marginal Plate
11th Marginal Plate
12th Marginal Plate
1st Neural Plate
2nd Neural Plate
3rd Neural Plate
4th Neural Plate
5th Neural Plate
6th Neural Plate
7th Neural Plate
8th Neural Plate
1st Supra Caudal
2nd Supra Caudal
Pygal Plate
4.


hyoplastral bridge.
sutural connection.
hypoplastral bridge.
epiplastron.
hyoplastron
hypoplastron
hyphyplastron
entoplastron
epiplastron.
cut edge of plastron
6.


Premax.
Max.
Prefront.
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Ant.pt.
of T.F.
Jug.
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Qu-ju.
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Art.pt.qu.
Squam.
Par.
Temp.fo.
Lat.bo.
Tym.rec.
Sup.occ.
Occ.cr.
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2.
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Pt.fr.
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Pr.zyg.
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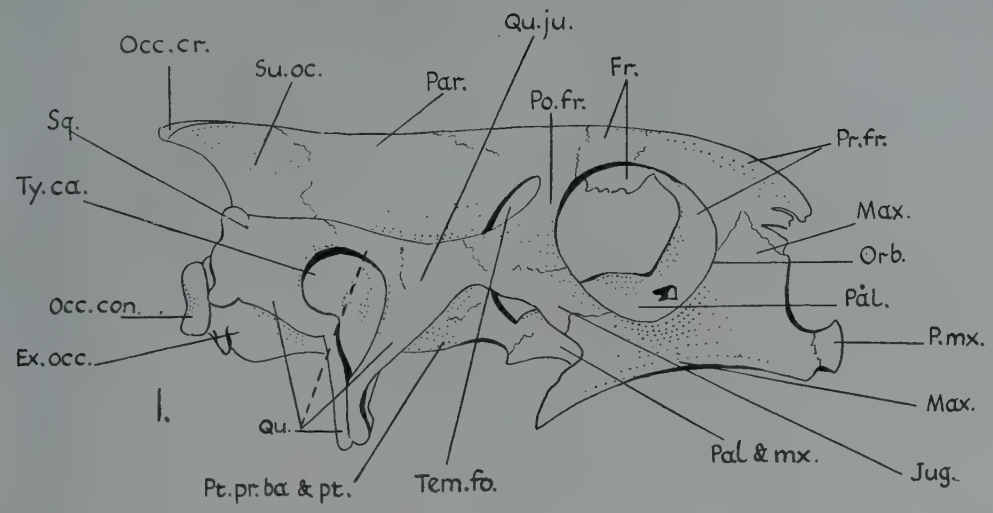
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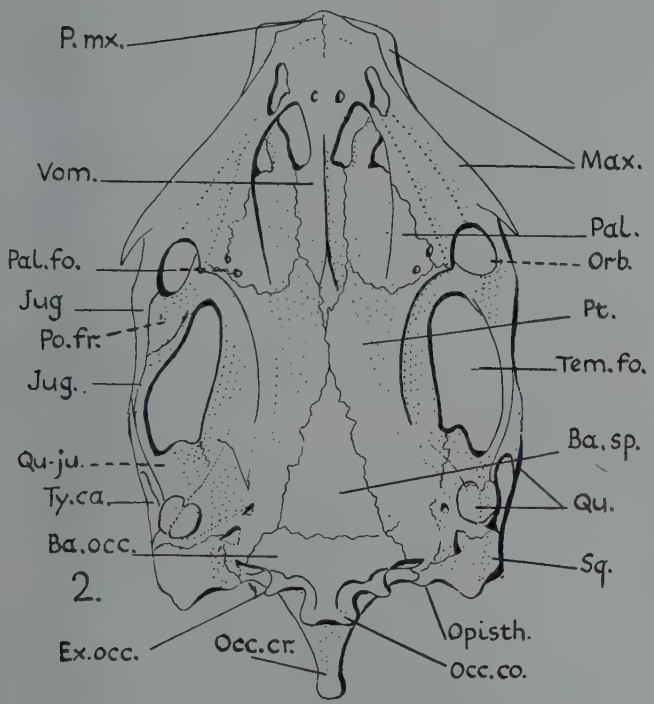
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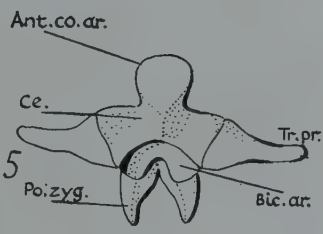
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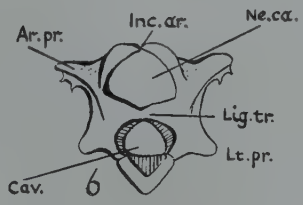
Po.zyg.
Bic.ar.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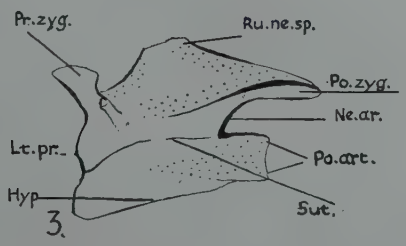
6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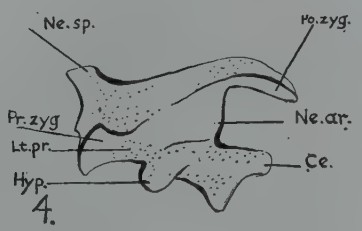
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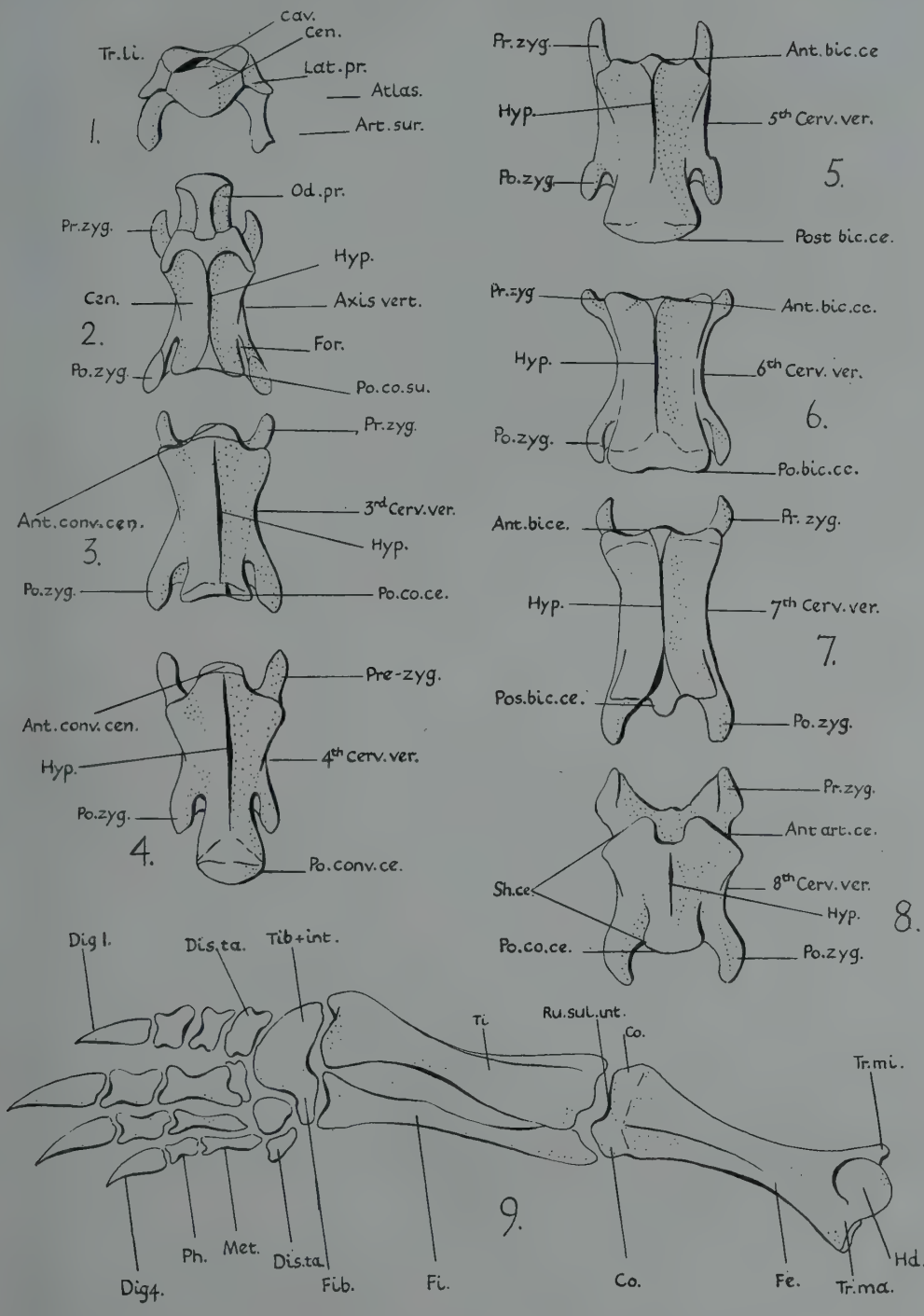
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Po.co.su.
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Ant.conv.cen.
3rd Cerv.ver.
Hyp.
3.
Po.zyg.
Po.co.ce.
Pre-zyg.
Ant.conv.cen.
Hyp.
4th cerv.ver.
Po.zyg.
4.
Po.conv.ce.
Pr.zyg.
Ant.bic.ce
Hyp.
5th Cerv.ver.
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Pr.zyg
Ant.bic.ce.
Hyp.
6th Cerv. ver.
Po.zyg.
6.
Po.bic.ce.
Ant.bice.
Pr. zyg.
Hyp.
7th Cerv.ver.
7.
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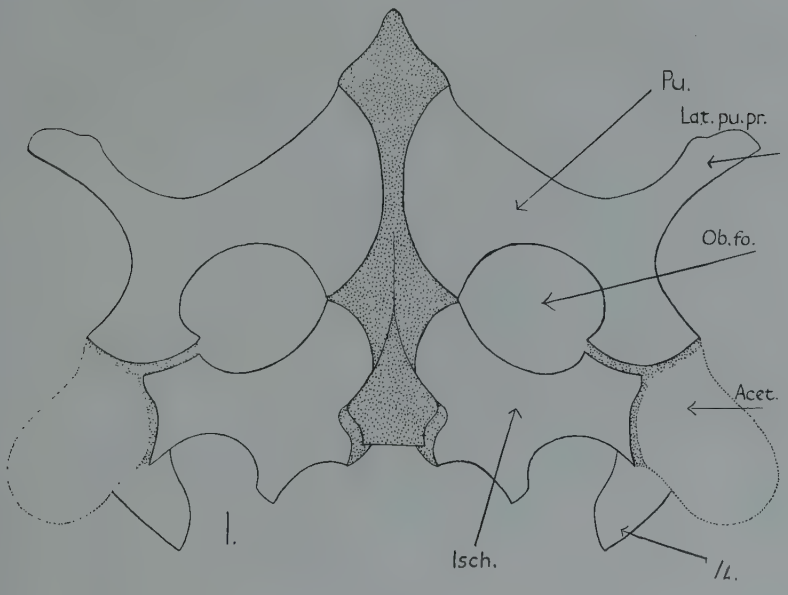
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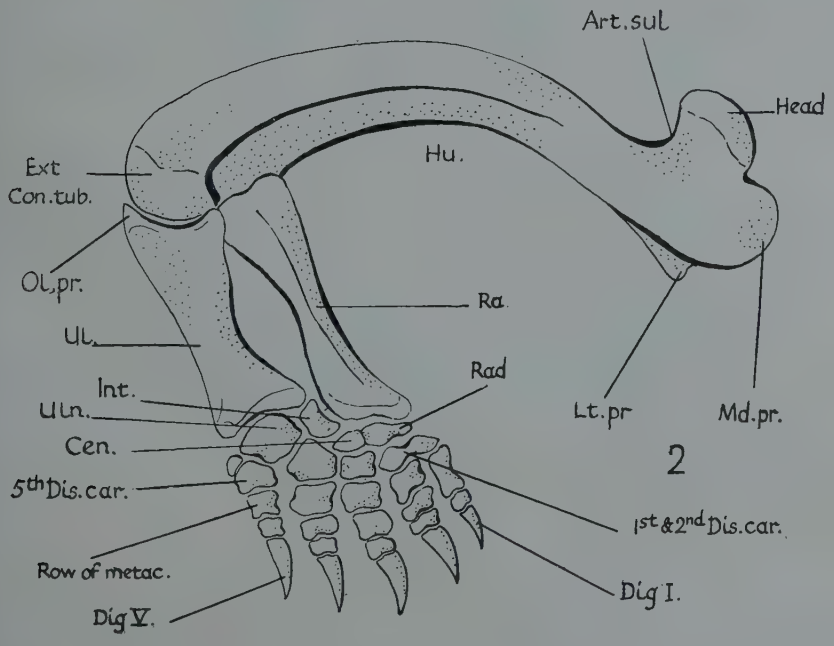
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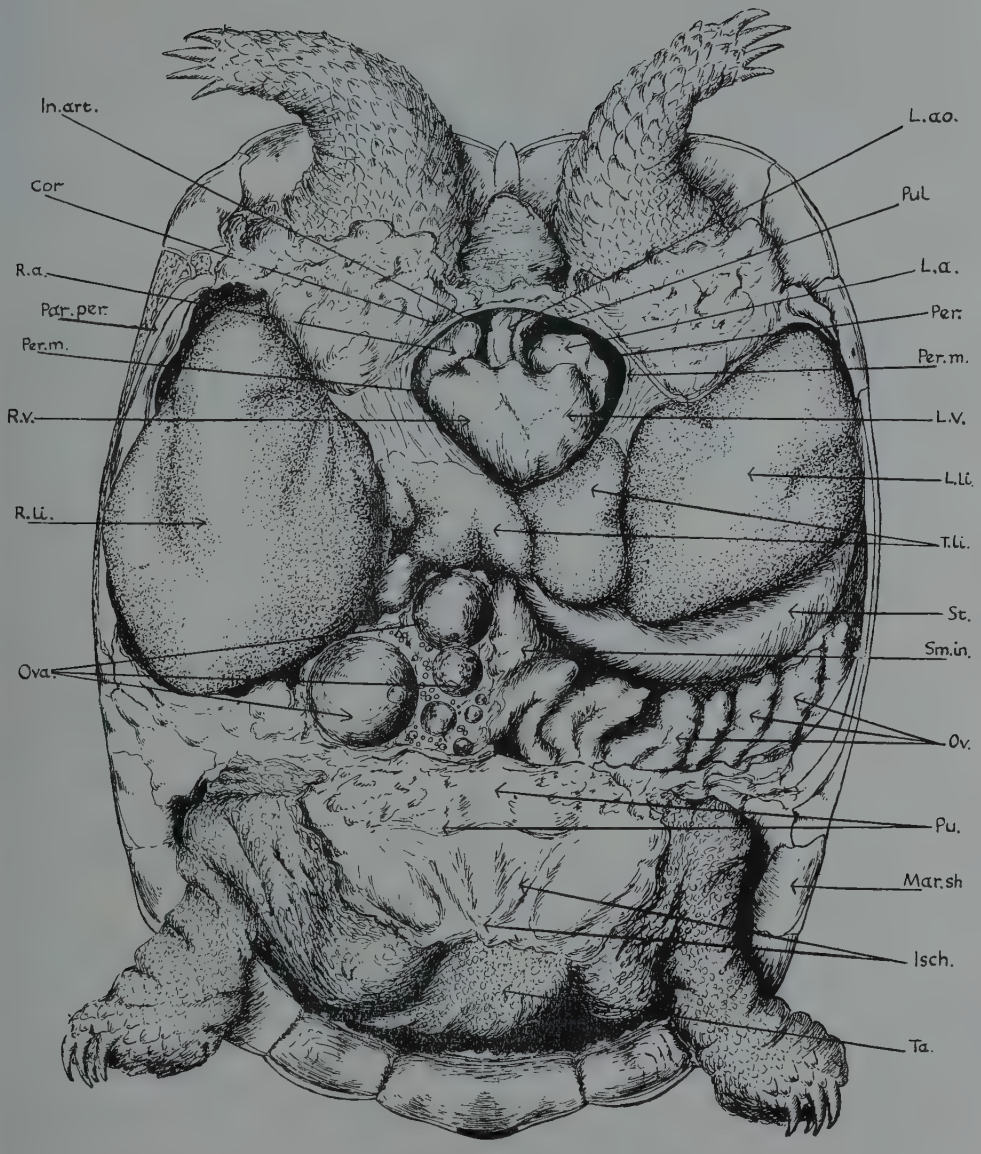
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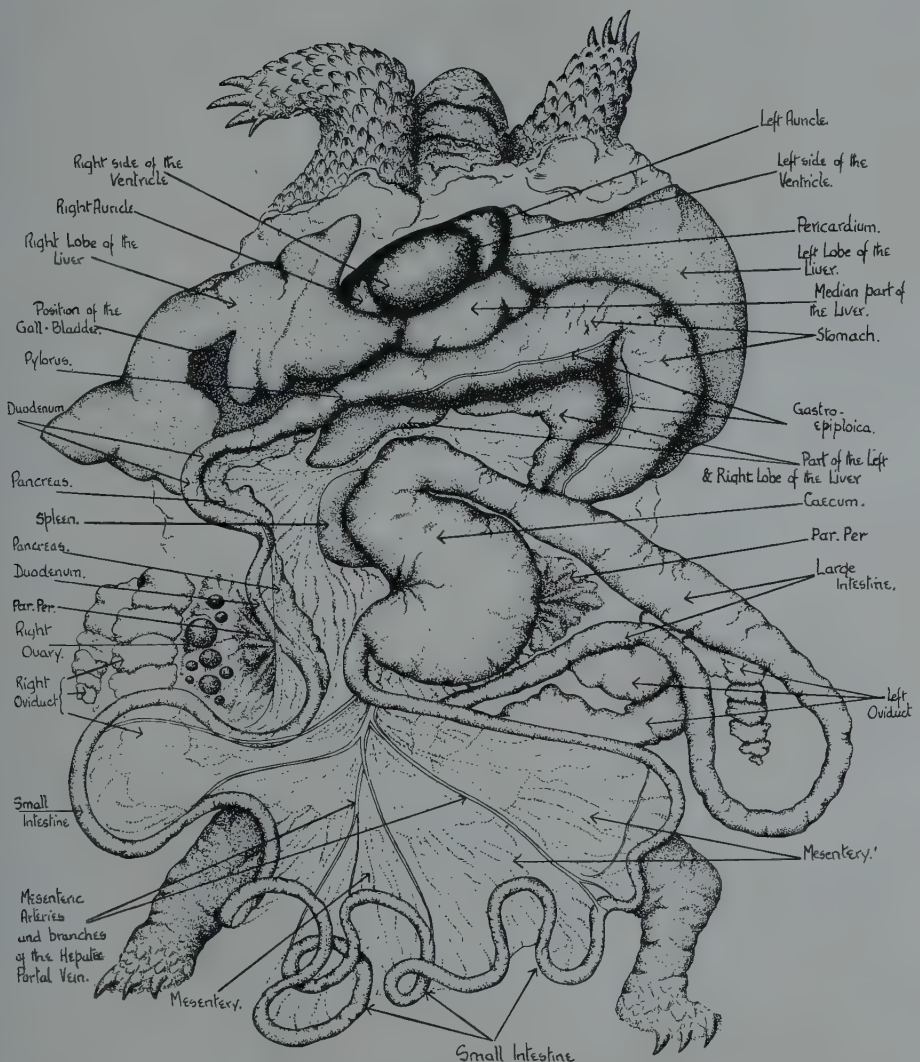
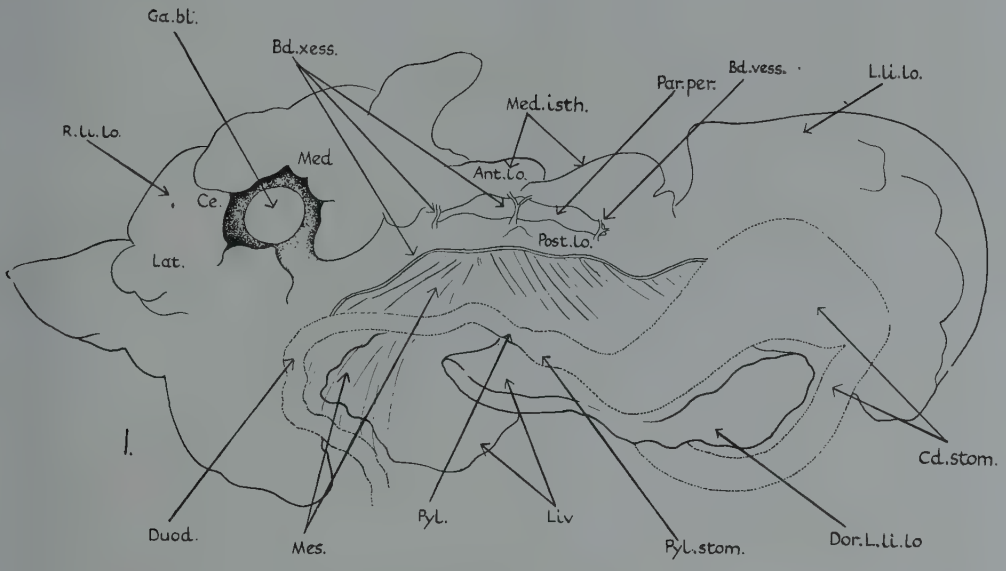

Left Auricle.
Left side of the Ventricle.
Right side of the Ventricle
Right Auricle
Right Lobe of the Liver
Pericardium.
Left Lobe of the Liver.
Median part of the Liver.
Position of the Gall-Bladder.
Stomach.
Pylorus.
Duodenum
Gastro-epiploica.
Part of the Left & Right Lobe of the Liver
Pancreas.
Caecum.
Spleen.
Par. Per
Pancreas.
Large Intestine.
Duodenum.
Par. Per.
Right Ovary.
Right Oviduct
Left Oviduct
Small Intestine
Mesentery.
Mesenteric Arteries and branches of the Hepatic Portal Vein.
Mesentery.
Small Intestine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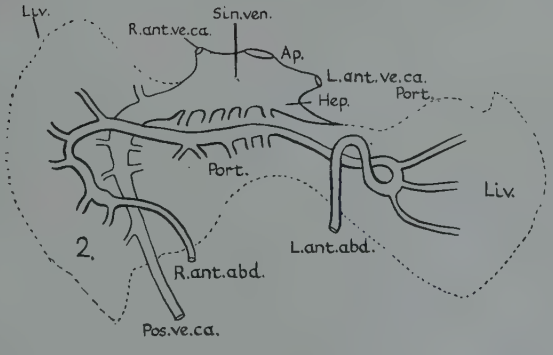
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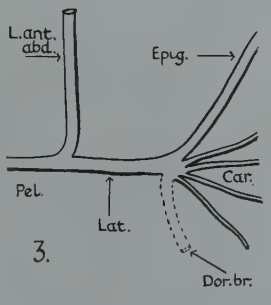
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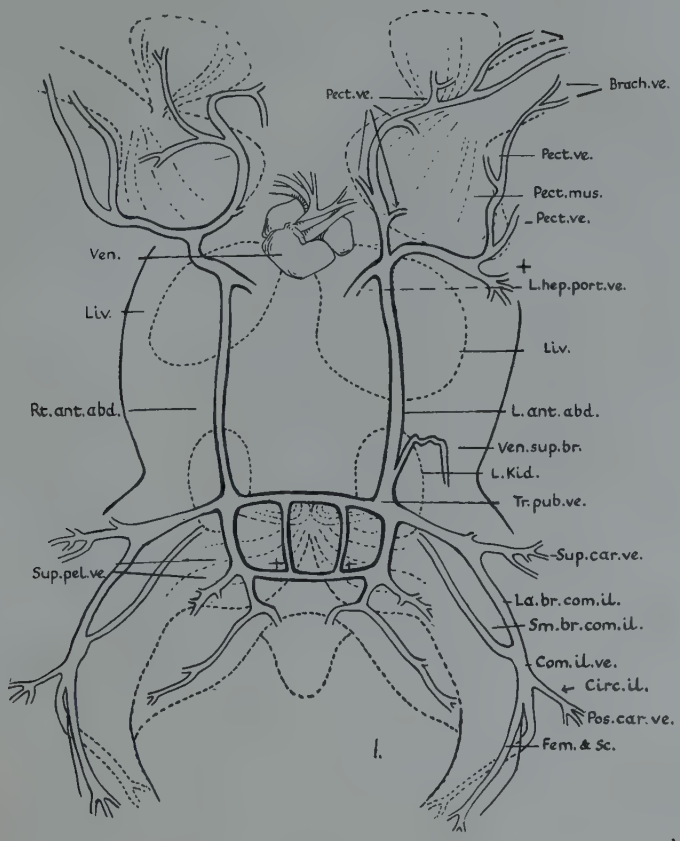
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Ven.sup.br.
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Sup.car.ve.
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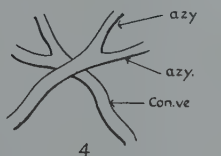
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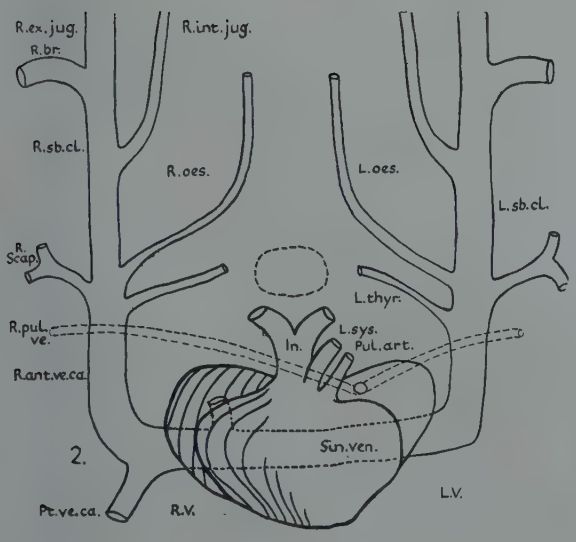
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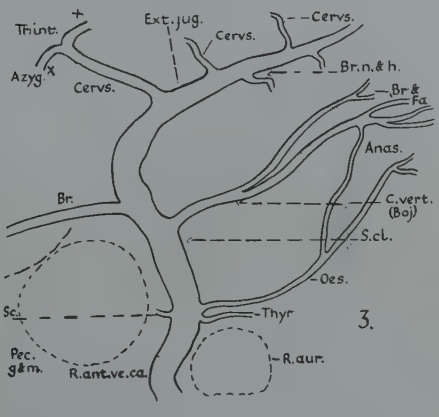
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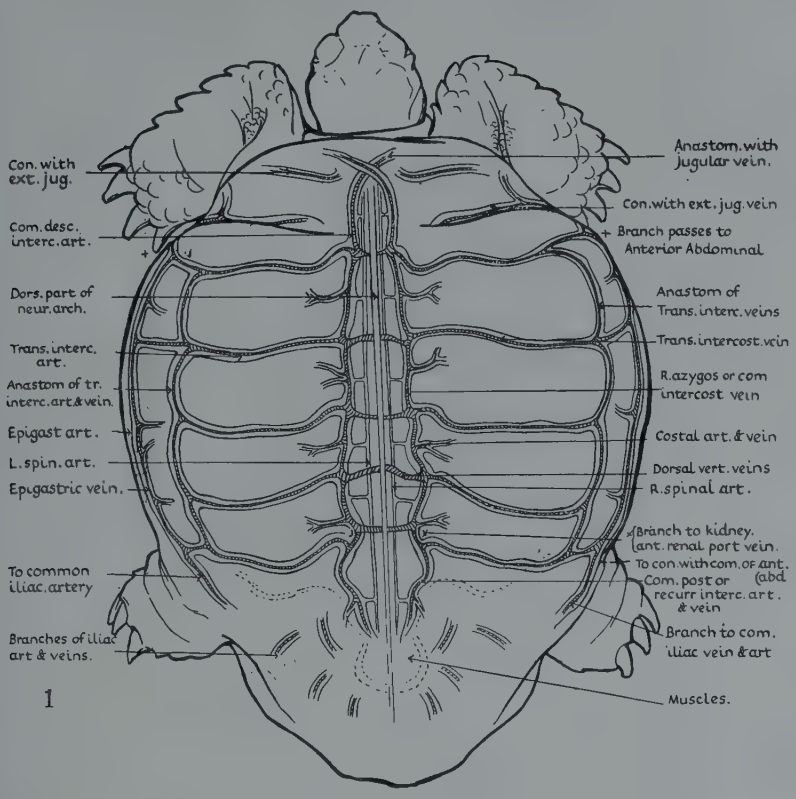
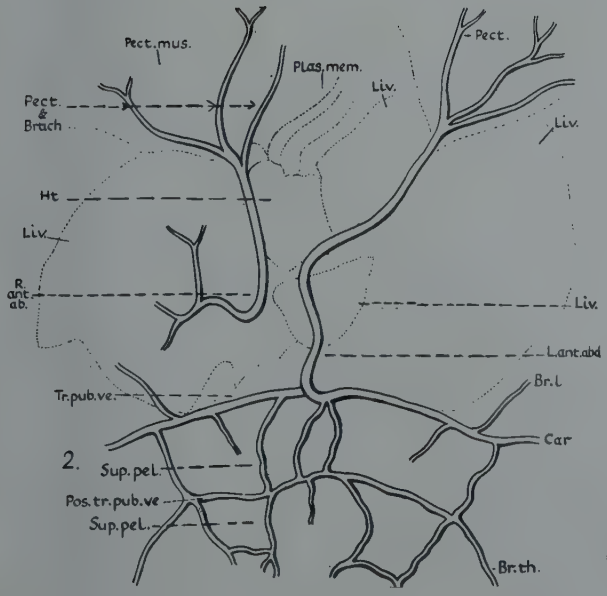
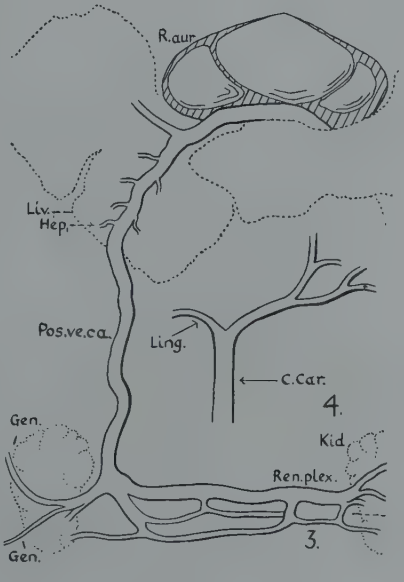
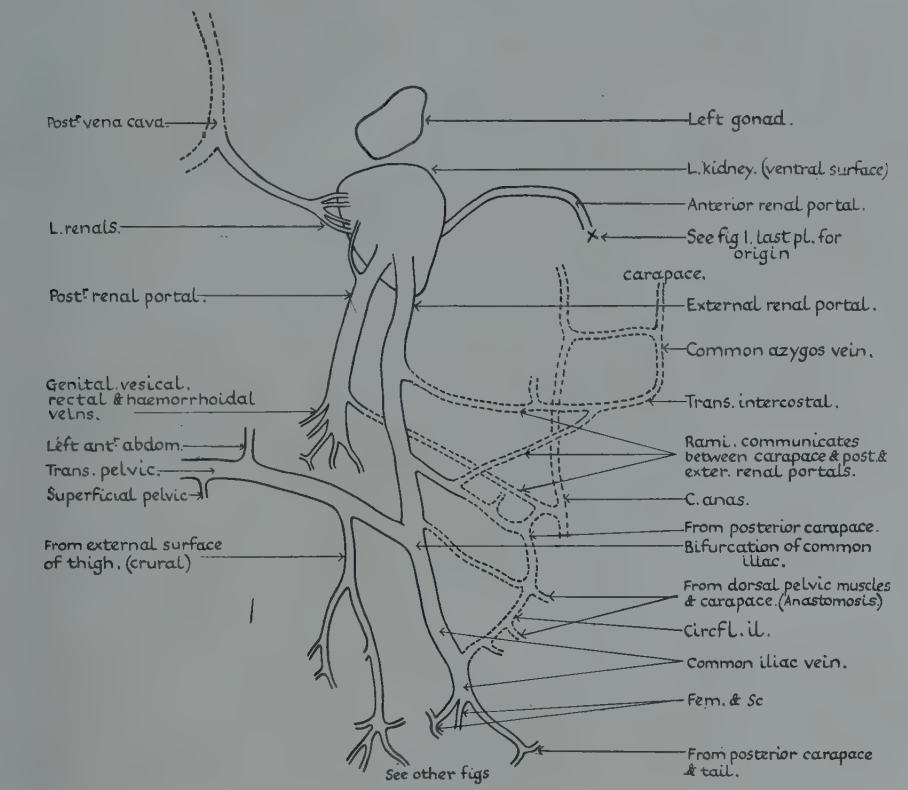
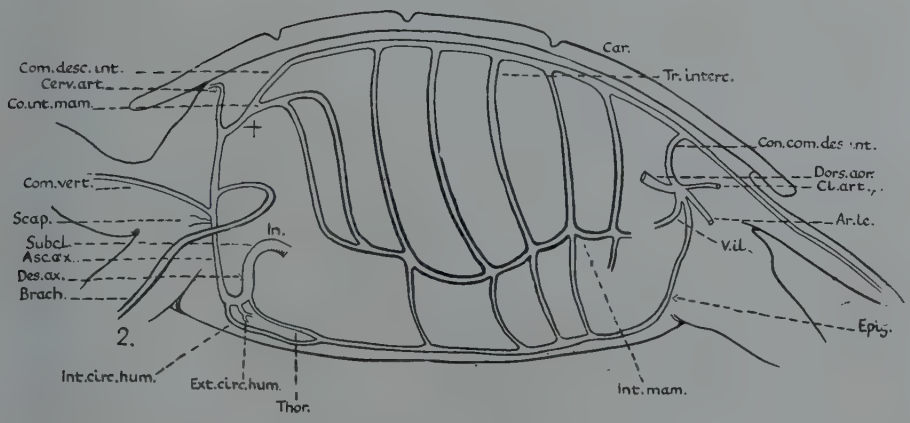
Anas.
Br.
C.vert. (Baj)
S.cl.
Oes.
Sc.
Thyr
3.
Pec. g&m.
R.ant.ve.ca.
R.aur.

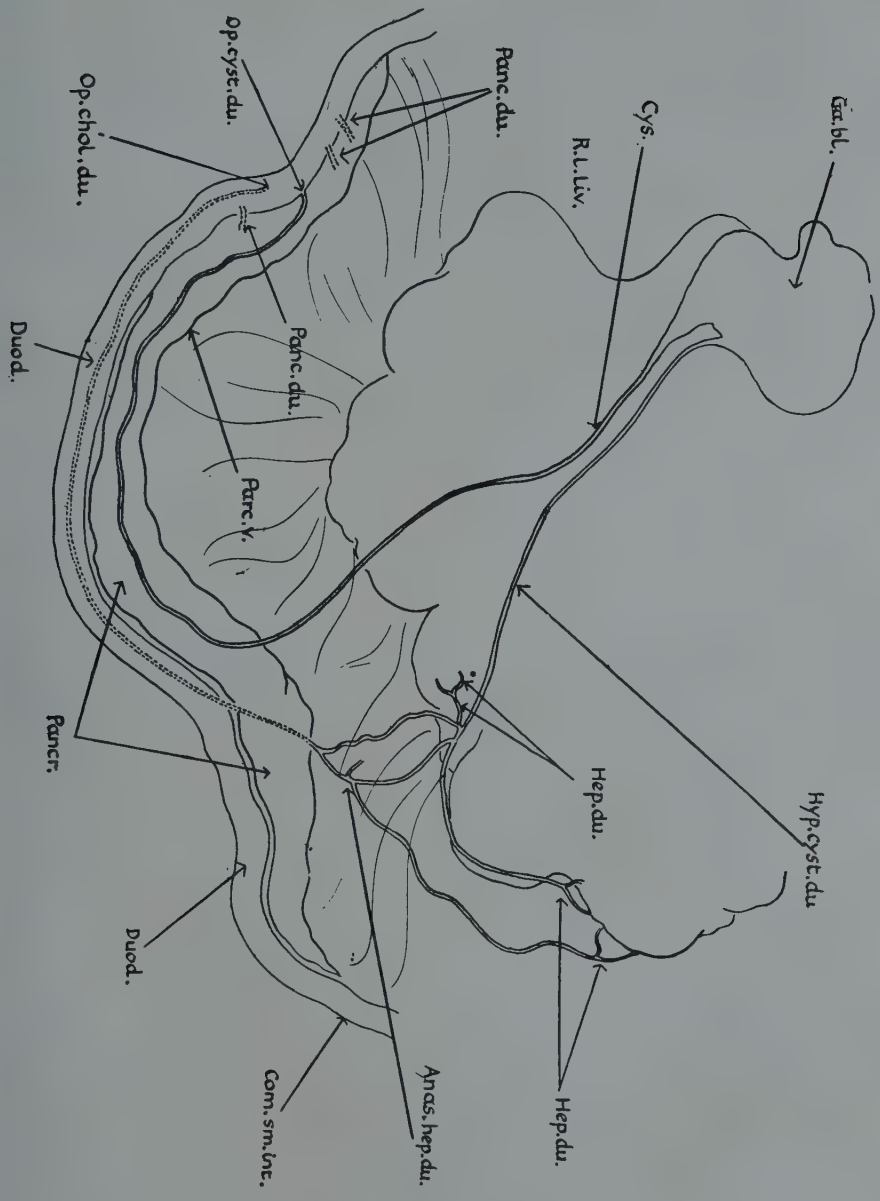

Con. with ext. jug.
Com. desc. interc. art.
Dors. part of neur. arch.
Trans. interc. art.
Anastom of tr. interc. art & vein.
Epigast art.
L. spin. art.
Epigastric vein.
To common iliac. artery
Branches of iliac art & veins.
Anastom. with Jugular vein.
Con. with ext. jug. vein
Branch passes to Anterior Abdominal
Anastom of Trans. interc. veins
Trans. intercost. vein
R. azygos or com intercost vein
Costal art. & vein
Dorsal vert. veins
R. spinal art.
Branch to kidney.
(ant. renal port vein.
To con. with com. or ant.
Com. post or (abd
recurr interc. art.
& vein
Branch to com.
iliac vein & art
Muscles.
1

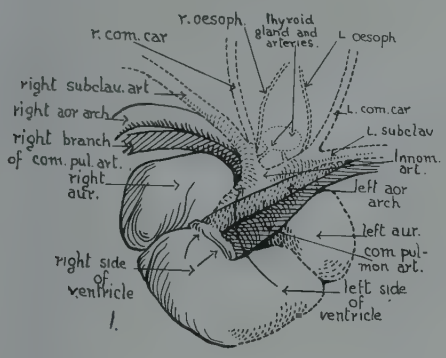

Pect. mus.
Plas. mem.
Liv.
Pect.
Pect. & Brach
Liv.
Ht
Liv.
R. ant. ab.
Liv.
L. ant. abd
Br. L
Tr. pub. ve.
Car
2.
Sup. pel.
Pos. tr. pub. ve
Sup. pel.
Br. th.

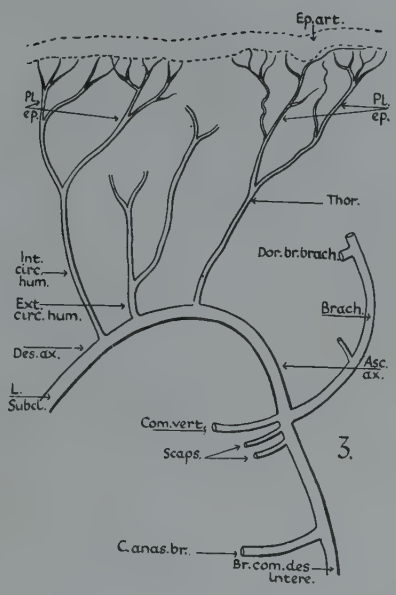

R. aur.
Liv.
Hep.
Pos. ve. ca.
Ling.
C. Car.
4.
Gen.
Kid.
Ren. plex.
3.
Gen.

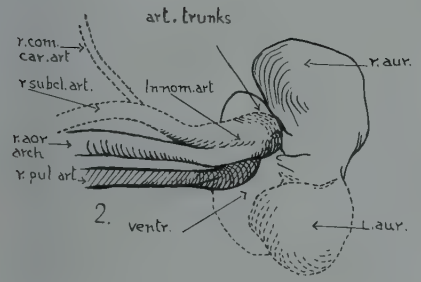

Post^r vena cava.
Left gonad.
L. kidney. (ventral surface)
Anterior renal portal.
See fig 1. last pl. for origin
L. renals.
carapace.
Post^r renal portal.
External renal portal.
Common azygos vein.
Genital. vesical. rectal & haemorrhoidal veins.
Trans. intercostal.
Left ant^r abdom.
Trans. pelvic.
Superficial pelvic
Rami. communicates between carapace & post.& exter. renal portals.
C. anas.
From posterior carapace.
From external surface of thigh. (crural)
Bifurcation of common iliac.
From dorsal pelvic muscles & carapace. (Anastomosis)
Circfl. il.
Common iliac vein.
Fem. & Sc
From posterior carapace & tail.
See other figs
1

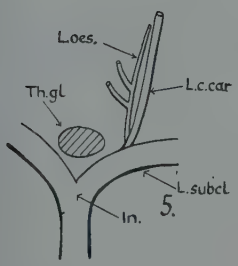

Car.
Com.desc. int.
Tr. interc.
Cerv. art.
Co. int. mam.
Con. com. des. int.
Dors. aor.
Com. vert.
Cl. art.
Scap.
Ar. le.
In.
Subcl.
V. il.
Asc. ax.
Des. ax.
Brach.
Epig.
2.
Int. circ. hum.
Ext. circ. hum.
Thor.
Int. mam.

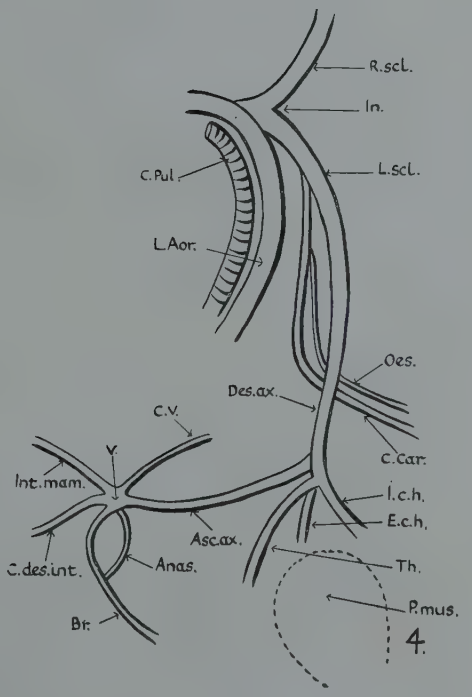

Gall.bl.
Cys.
R.l.liv.
Panc.du.
Op.cyst.du.
Op.chol.du.
Duod.
Panc.du.
Panc.v.
Hyp.cyst.du
Hep.du.
Pancr.
Duod.
Hep.du.
Anas.hep.du.
Com.sm.int.

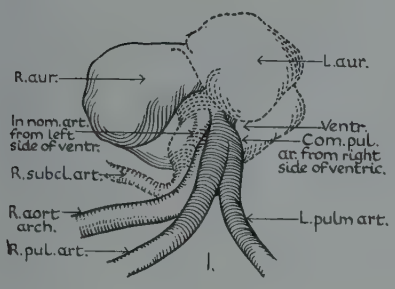

r. com. car
r. oesoph.
thyroid gland and arteries.
L. oesoph
right subclav. art
right aor arch
right branch of com. pul. art.
right aur.
L. com. car
L. subclav
Innom. art.
left aor arch
left aur.
com. pul-mon art.
left side of ventricle
right side of ventricle
1.

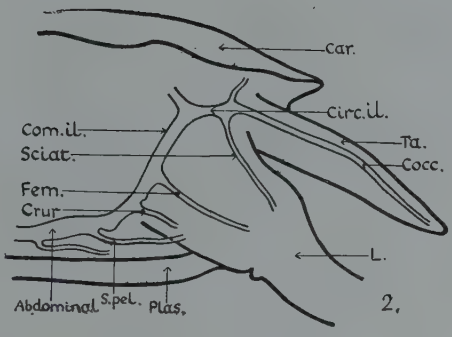

Ep. art.
Pl. ep.
Pl. ep.
Thor.
Dor. br. brach.
Int. circ. hum.
Ext. circ. hum.
Brach.
Des. ax.
Asc. ax.
L. Subcl.
Com. vert.
Scaps.
3.
C. anas. br.
Br. com. des lntere.

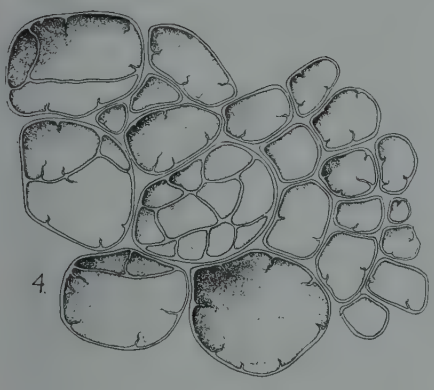

art. trunks
r. com. car. art
r. subcl. art.
In. nom. art
r. aor arch
r. pul art
r. aur.
2.
ventr.
L. aur.

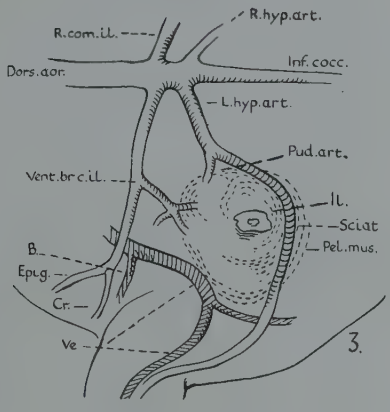

L. oes.
Th. gl
L. c. car
L. subcl
In.
5.

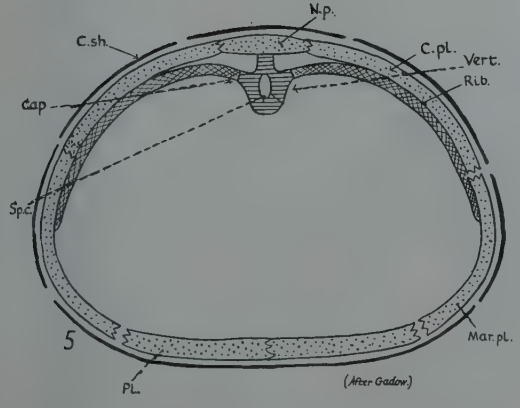

R. scl.
In.
L. scl.
C. Pul.
L. Aor.
Oes.
Des. ax.
C. V.
C. car.
V.
Int. mam.
I. c. h.
E. c. h.
Asc. ax.
C. des. int.
Anas.
Th.
P. mus.
Br.
4.

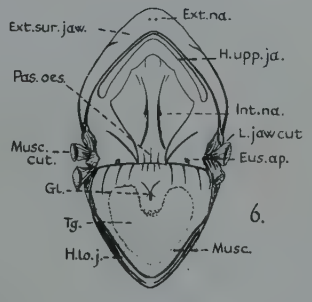

R.aur.
L.aur.
In nom.art. from left side of ventr.
Ventr.
Com.pul. ar. from right side of ventric.
R.subcl.art.
R.aort. arch.
L.pulm art.
R.pul.art.
1.

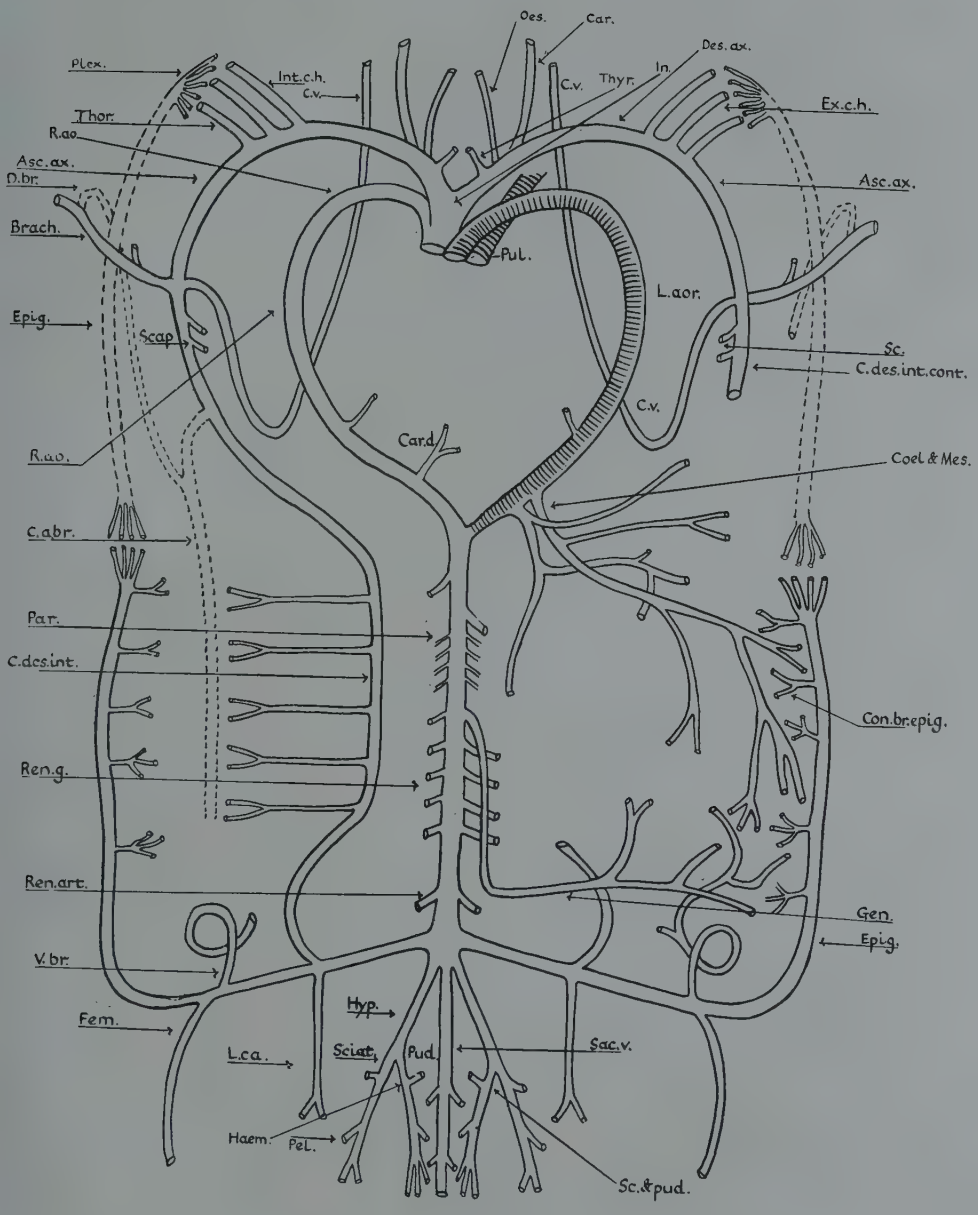

Car.
Circ.il.
Com.il.
Sciat.
Ta.
Cocc.
Fem.
Crur
L.
Abdominal
S.pel.
Plas.
2.

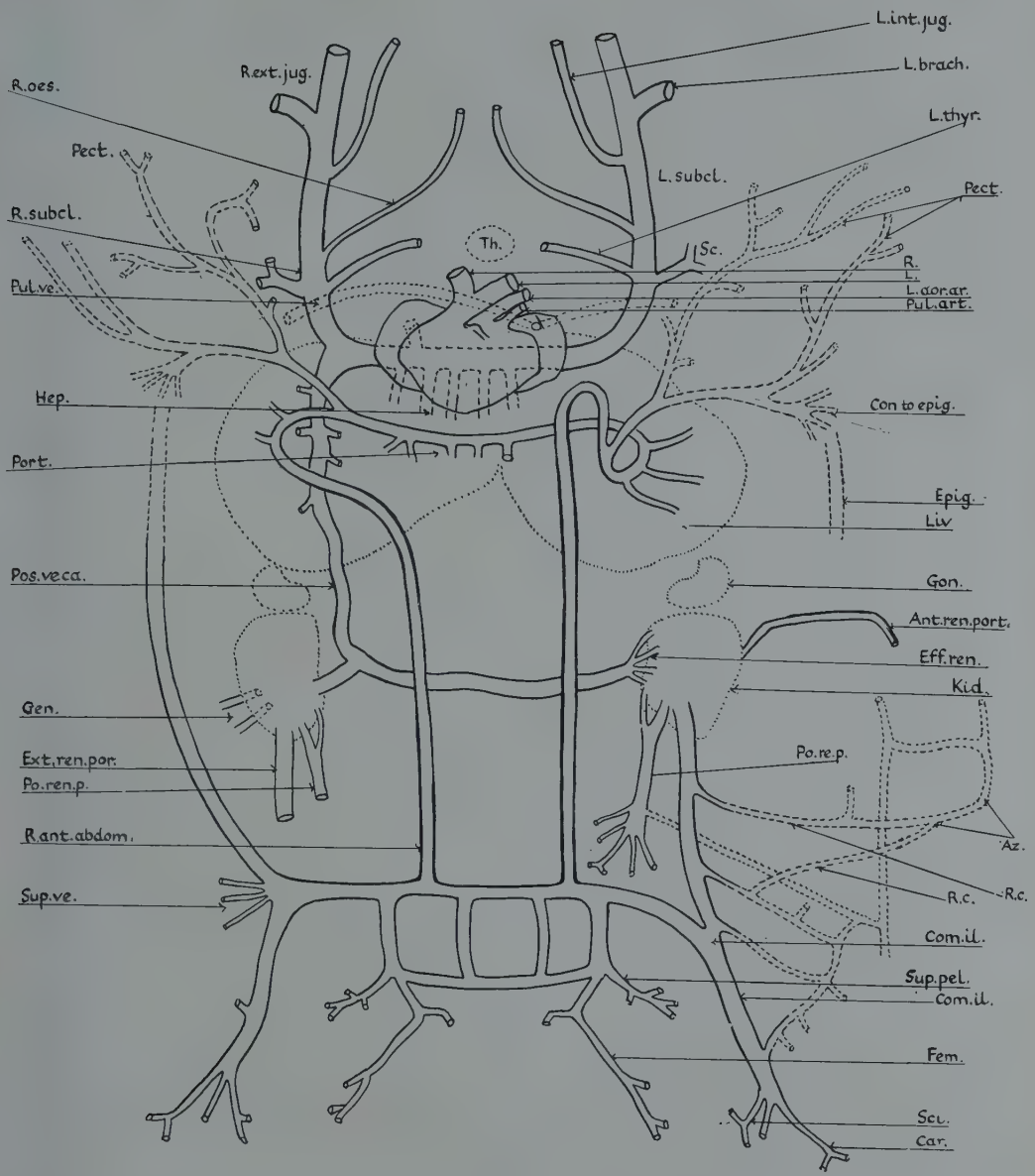

4.

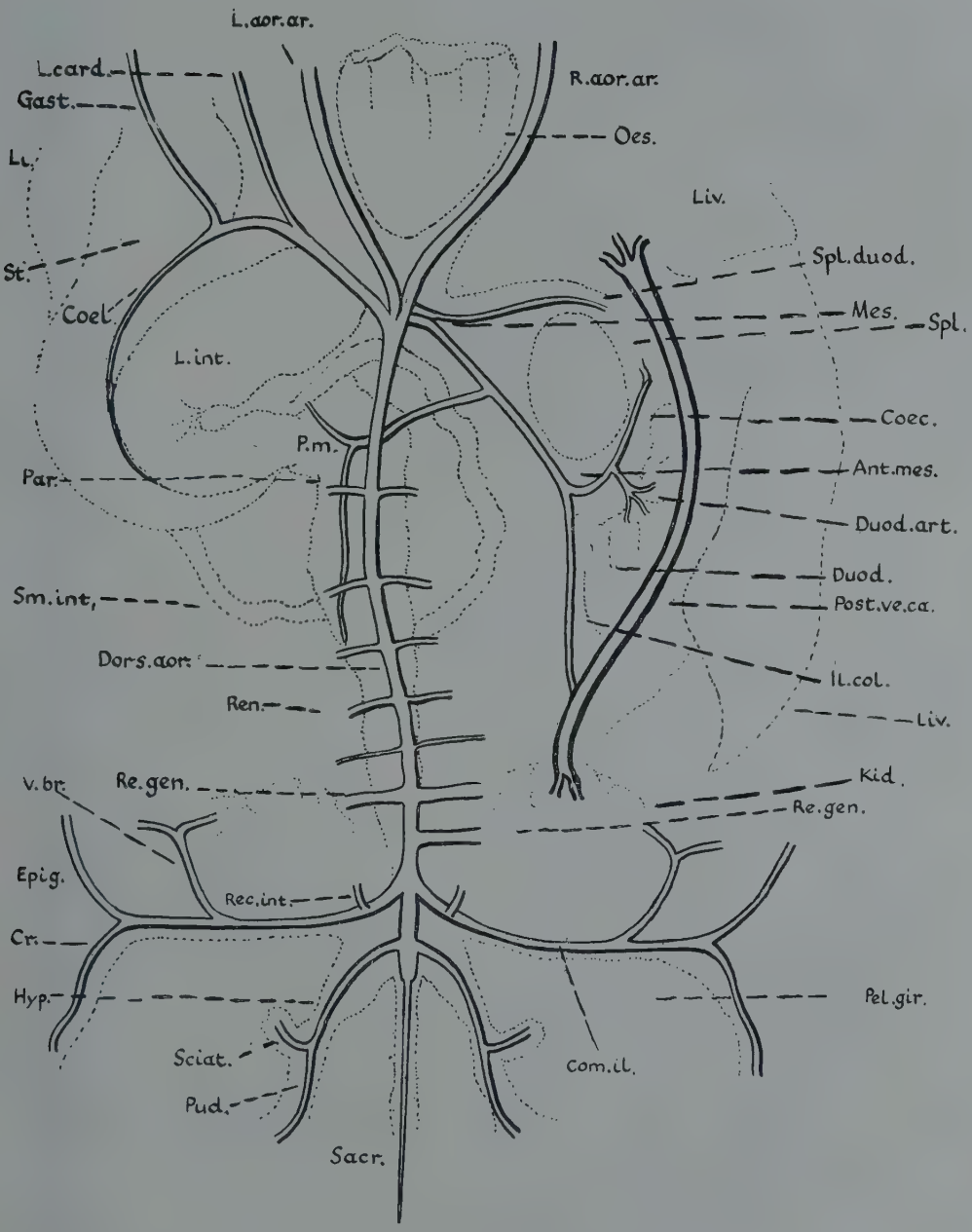

R.com.il.
R.hyp.art.
Inf. cocc.
Dors.aor.
L.hyp.art.
Pud.art.
Vent.br c.il.
Il.
Sciat
Pel.mus.
B.
Epig.
Cr.
Ve
3.

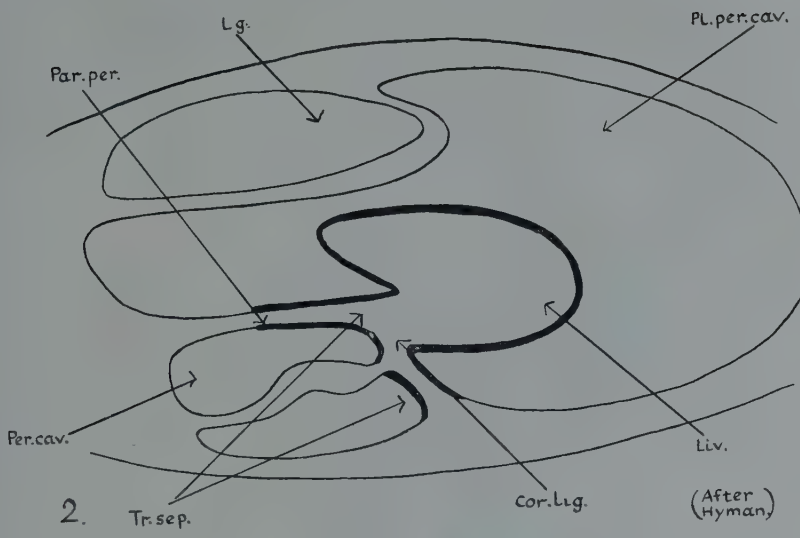

N.p.
C.sh.
C.pl.
Vert.
Rib.
Cap
Sp.c.
Mar.pl.
PL.
(After Gadow.)
5


Ext.sur.jaw.
Ext.na.
H.upp.ja.
Pas.oes.
Int.na.
L.jaw cut
Musc. cut.
Eus.ap.
Gl.
Tg.
H.lo.j.
Musc.
6.

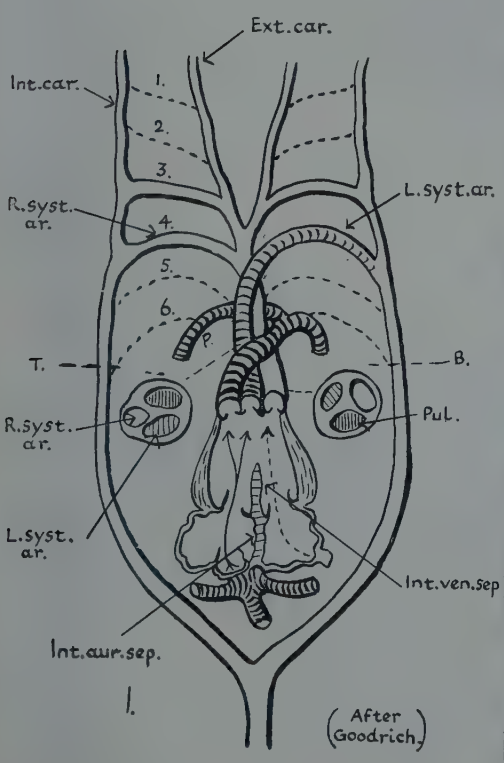

Oes.
Car.
Des. ax.
Plex.
Int.c.h.
C.v.
C.v.
Thyr.
In.
Ex.c.h.
Thor.
R.ao.
Asc.ax.
D.br.
Asc.ax.
Brach.
Pul.
L.aor.
Epig.
Scap.
Sc.
C.des.int.cont.
C.v.
Card.
R.ao.
Coel & Mes.
C.abr.
Par.
C.des.int.
Con.br.epig.
Ren.g.
Ren.art.
Gen.
Epig.
V.br.
Hyp.
Fem.
L.ca.
Sciat.
Pud.
Sac.v.
Haem.
Pel.
Sc.&pud.


L.int.jug.
L.brach.
L.thyr.
R.ext.jug.
R.oes.
Pect.
L.subcl.
Pect.
R.subcl.
Th.
Sc.
R.
L.
L.cor.ar.
Pul.ve.
Pul.art.
Hep.
Con to epig.
Port.
Epig.
Liv
Pos.veca.
Gon.
Ant.ren.port.
Eff.ren.
Kid.
Gen.
Ext.ren.por.
Po.re.p.
Po.ren.p.
Az.
R.ant.abdom.
R.c.
R.c.
Sup.ve.
Com.il.
Sup.pel.
Com.il.
Fem.
Scu.
Car.


L.aor.ar.
L.card.
Gast.
Li.
St.
Coel.
L.int.
P.m.
Par.
Sm.int.
Dors.aor.
Ren.
V.br.
Re.gen.
Epig.
Rec.int.
Cr.
Hyp.
Sciat.
Pud.
Sacr.
R.aor.ar.
Oes.
Liv.
Spl.duod.
Mes.
Spl.
Coec.
Ant.mes.
Duod.art.
Duod.
Post.ve.ca.
Il.col.
Liv.
Kid.
Re.gen.
Pel.gir.
Com.il.

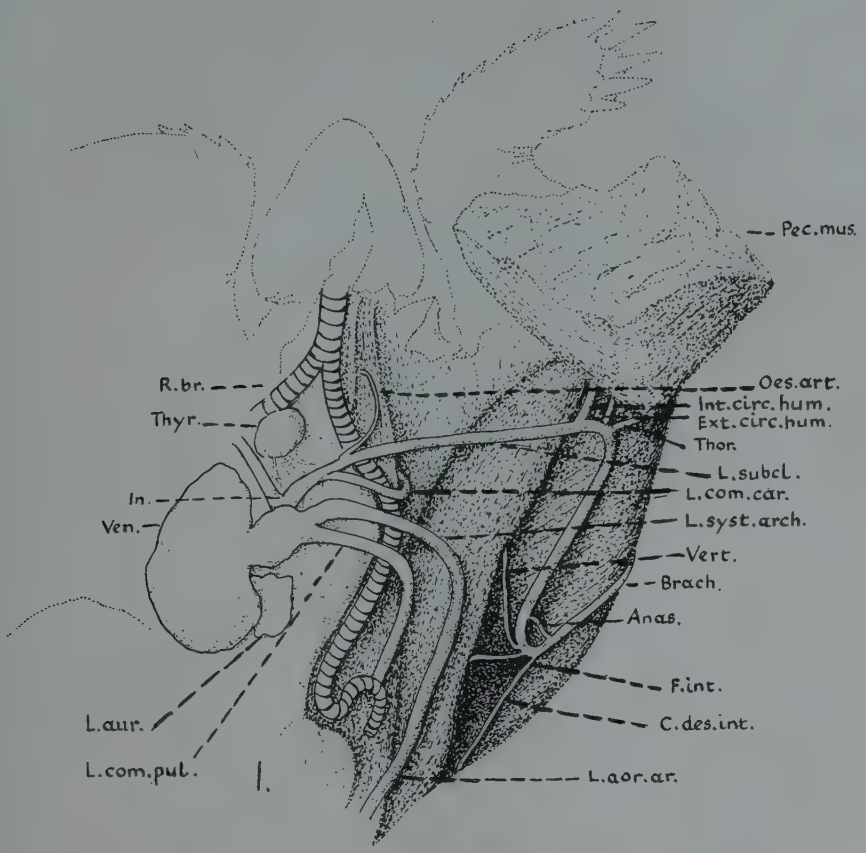

Lg.
Pl.per.cav.
Par.per.
Per.cav.
Liv.
Cor.Lg.
Tr.sep.
(After Hyman)

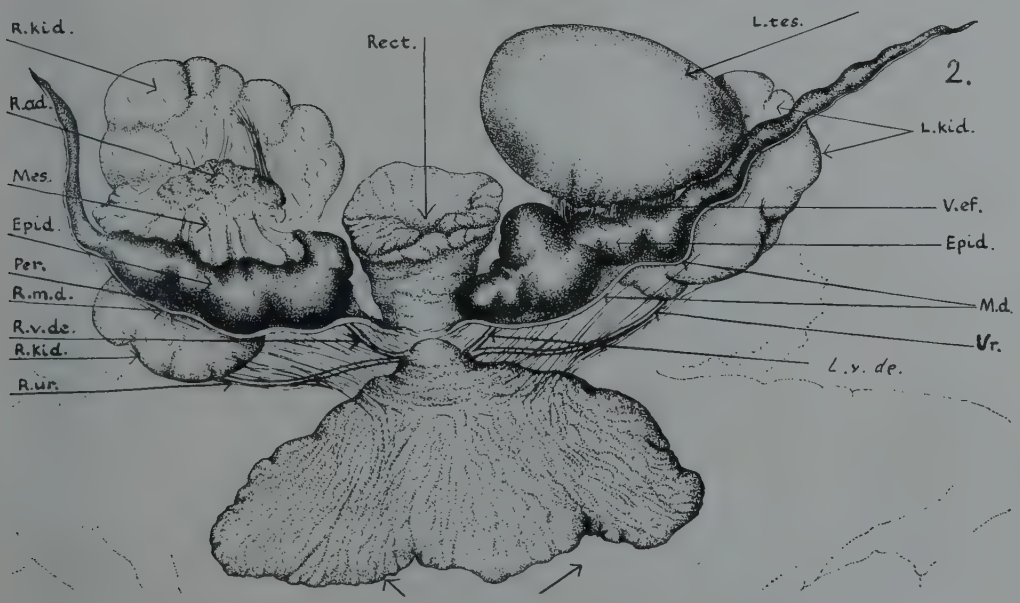
2.

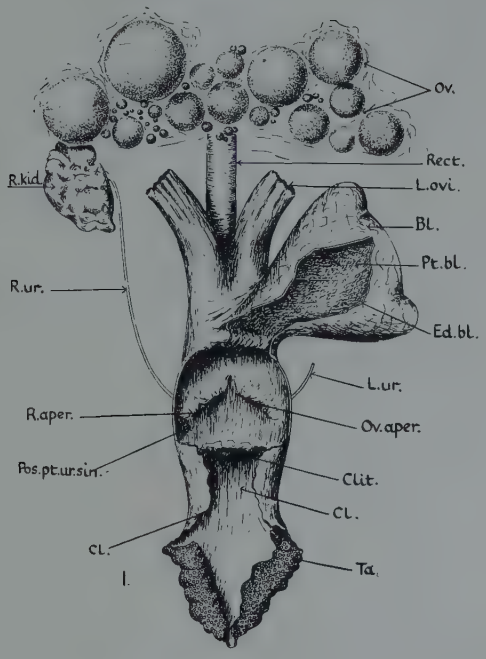

Ext.car.
Int.car.
1.
2.
3.
4.
5.
6.
R.syst. ar.
L.syst.ar.
P.
T.
B.
Pul.
R.Syst. ar.
L.Syst. ar.
Int.ven.sep
Int.aur.sep.
(After Goodrich)

1.

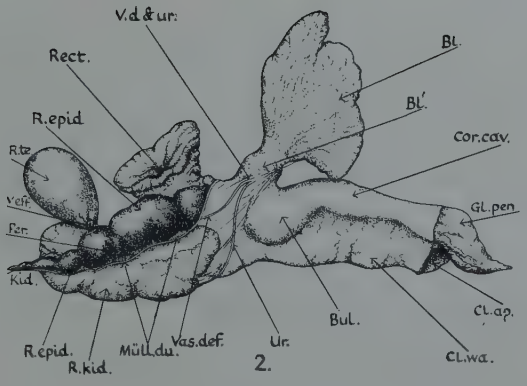
3.


Pec.mus.
R.br.
Thyr.
In.
Ven.
Oes.art.
Int.circ.hum.
Ext.circ.hum.
Thor.
L.subcl.
L.com.car.
L.syst.arch.
Vert.
Brach.
Anas.
F.int.
C.des.int.
L.aur.
L.com.put.
L.aor.ar.
1.


R.kid.
R.ad.
Mes.
Epid.
Per.
R.m.d.
R.v.de.
R.kid.
R.ur.
Rect.
L.tes.
L.kid.
V.ef.
Epid.
M.d.
Vr.
L.v.de.
2.

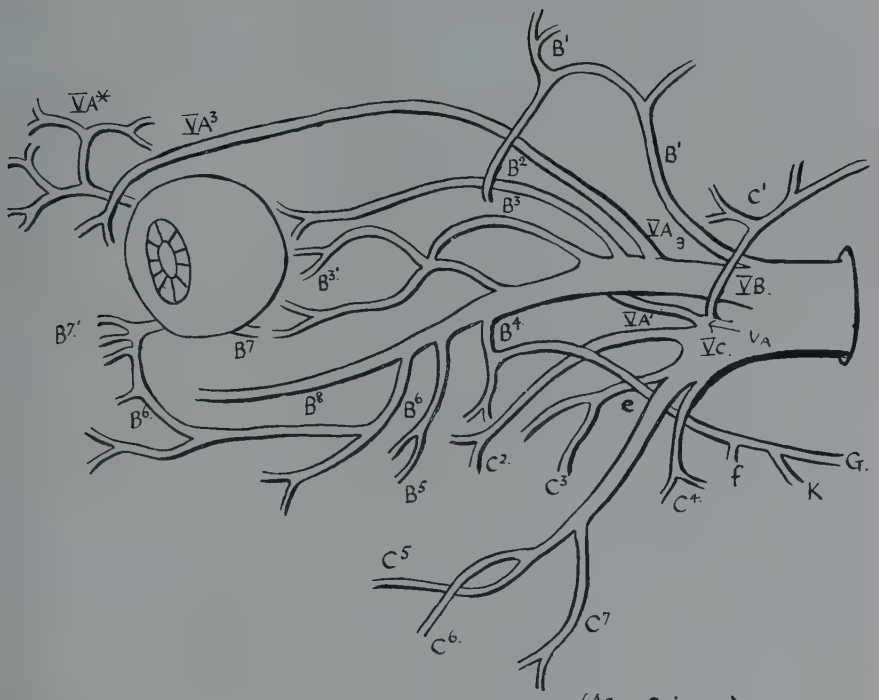

Ov.
Rect.
R.kid.
L.ovi.
Bl.
Pt.bl.
R.ur.
Ed.bl.
L.ur.
R.aper.
Ov.aper.
Pos.pt.ur.sin.
Clit.
Cl.
Cl.
Ta.

1.

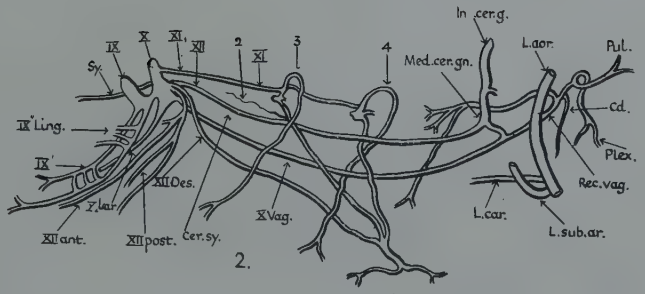

V.d.&ur.
Bl.
Rect.
Bl'.
R.epid.
Cor.cav.
R.te.
Gl.pen.
Vest.
Fer.
Kid.
Cl.ap.
Bul.
R.epid.
Vas.def.
Ur.
Cl.wa.
R.kid.
Müll.du.

2.

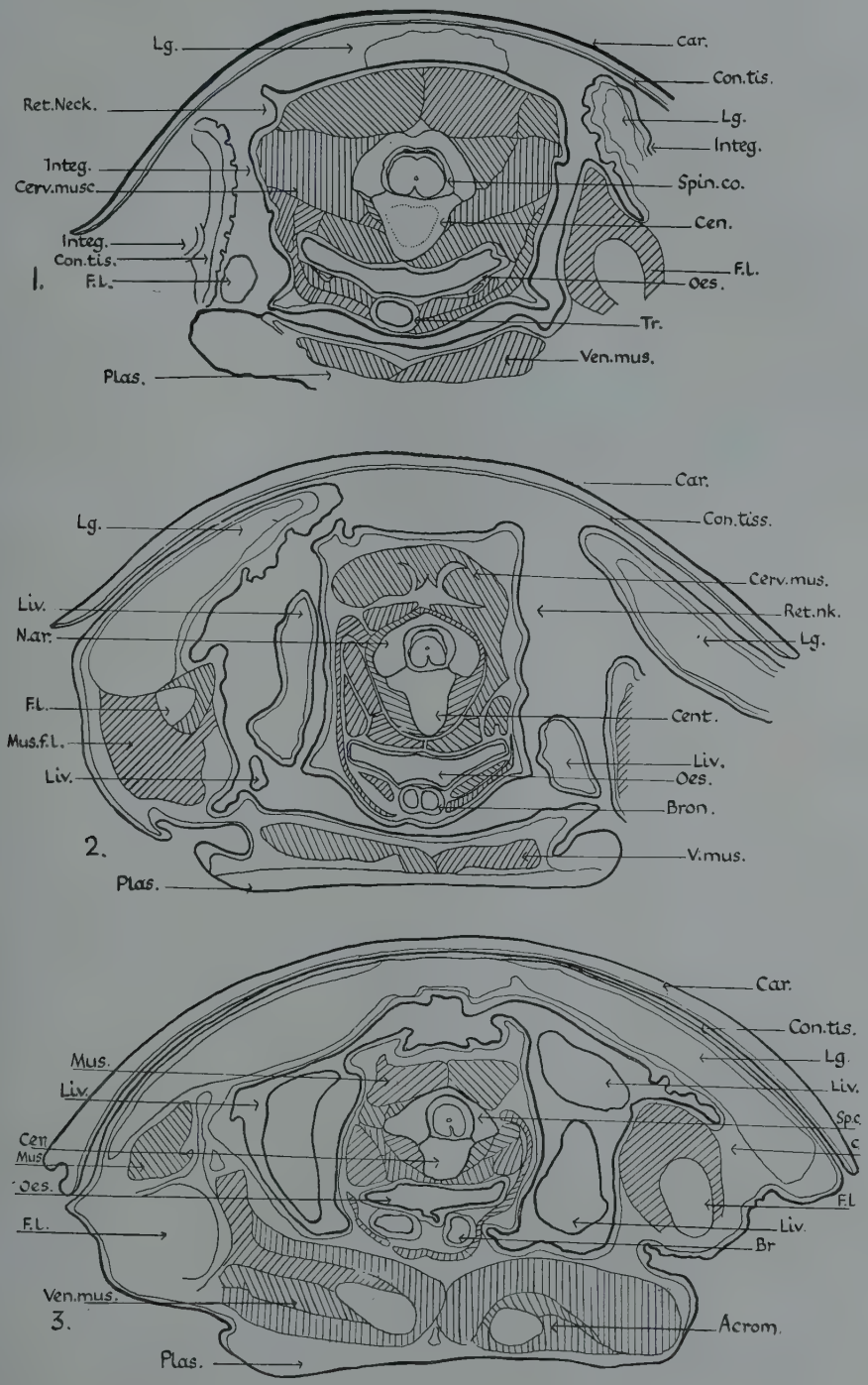
11.
19-21
Isch.
Crur.
18.
17.
Scplex.
16a.
15a
15.
14.
13.
12a
11a.
10
Mus
Sc.
9a
8a
7a
6a
5a
4a
3a
3
4.
5.
rad.
Uln
6
Med.
Rts.brplexus
Br.plexus
10
X
R.c
11
12
13
Sym.
14.
15
16.
Tib
(After Bojanus.)

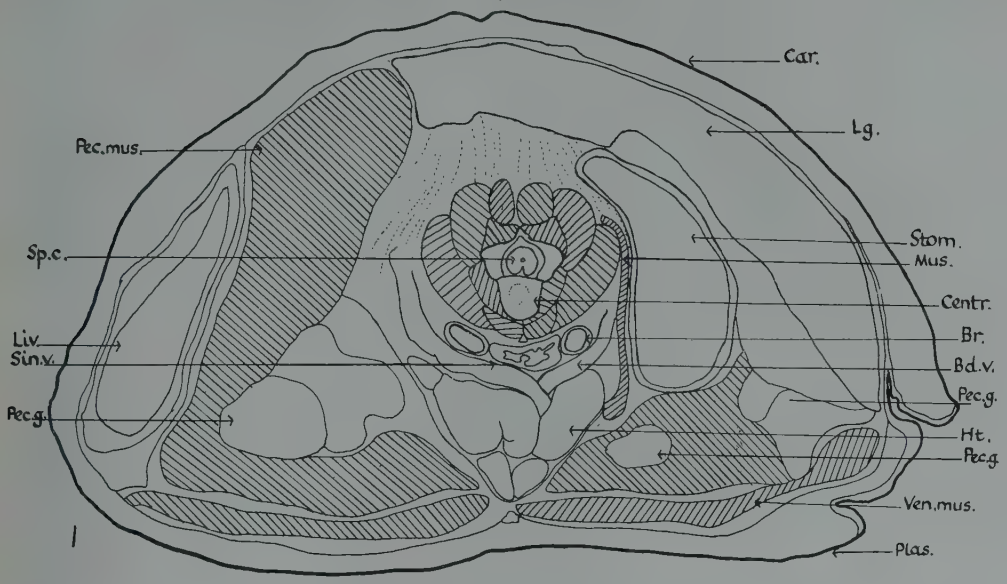


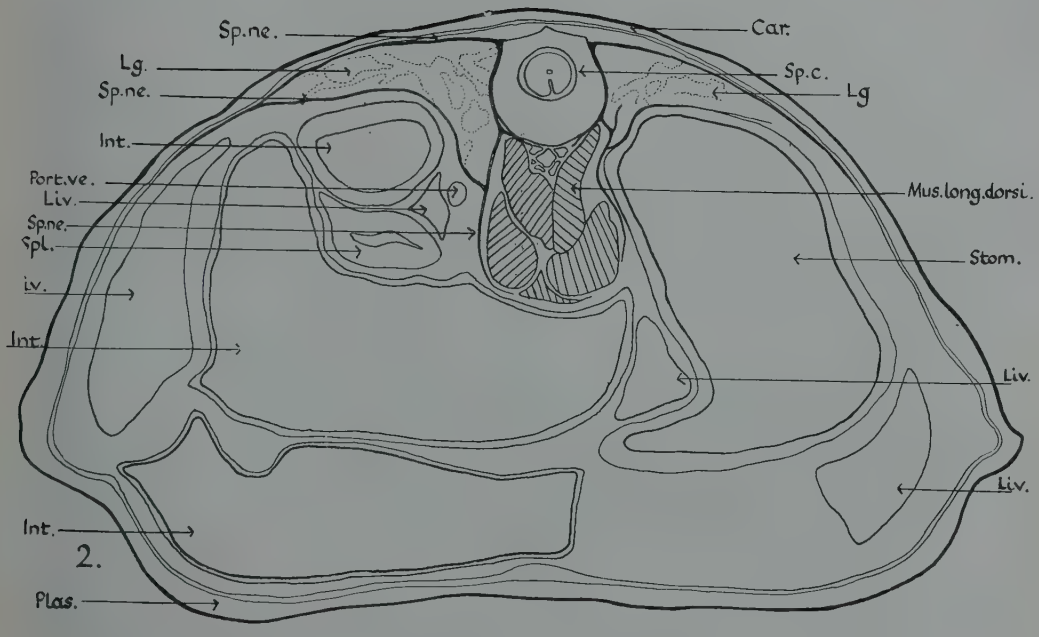
(After Bojanus.)

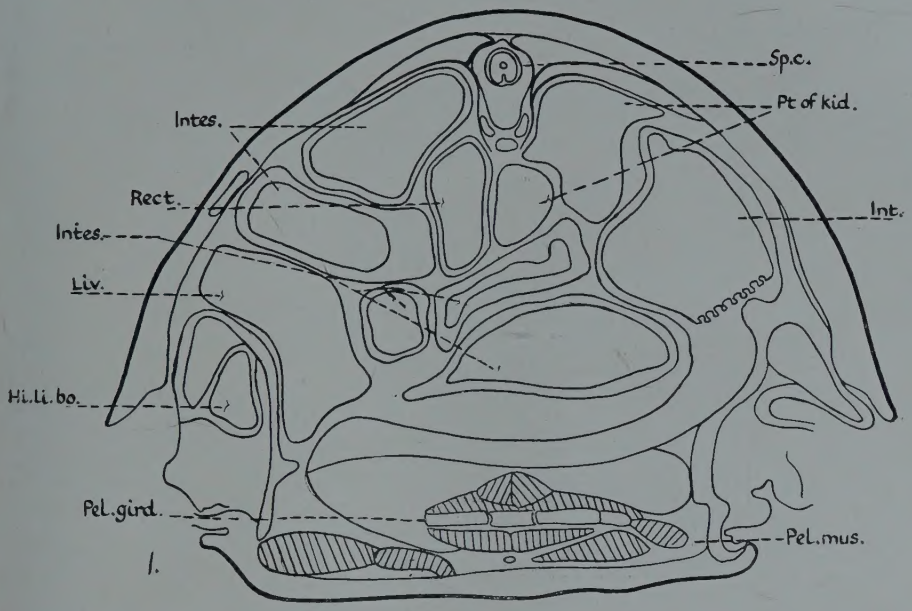


(After Bojanus.)


Lg.
Car.
Con.tis.
Ret.Neck.
Lg.
Integ.
Integ.
Cerv.musc.
Spin.co.
Cen.
Integ.
Con.tis.
F.L.
1.
F.L.
Oes.
Tr.
Ven.mus.
Plas.
Car.
Con.tiss.
Lg.
Cerv.mus.
Liv.
Ret.nk.
N.ar.
Lg.
F.L.
Cent.
Mus.f.L.
Liv.
Liv.
Oes.
Bron.
2.
V.mus.
Plas.
Car.
Con.tis.
Mus.
Lg.
Liv.
Liv.
Spc
Cen
Mus
C
Oes.
F.L
F.L.
Liv.
Br
Ven.mus.
3.
Acrom.
Plas.


Car.
Lg.
Pec.mus.
Stom.
Sp.c.
Mus.
Centr.
Br.
Liv.
Sin.v.
Bd.v.
Pec.g.
Pec.g.
Ht.
Pec.g.
Ven.mus.
Plas.
1


Sp.ne.
Car.
Lg.
Sp.c.
Sp.ne.
Lg
Int.
Port.ve.
Mus.long.dorsi.
Liv.
Sp.ne.
Spl.
Stom.
iv.
Int.
Liv.
Liv.
Int.
2.
Plas.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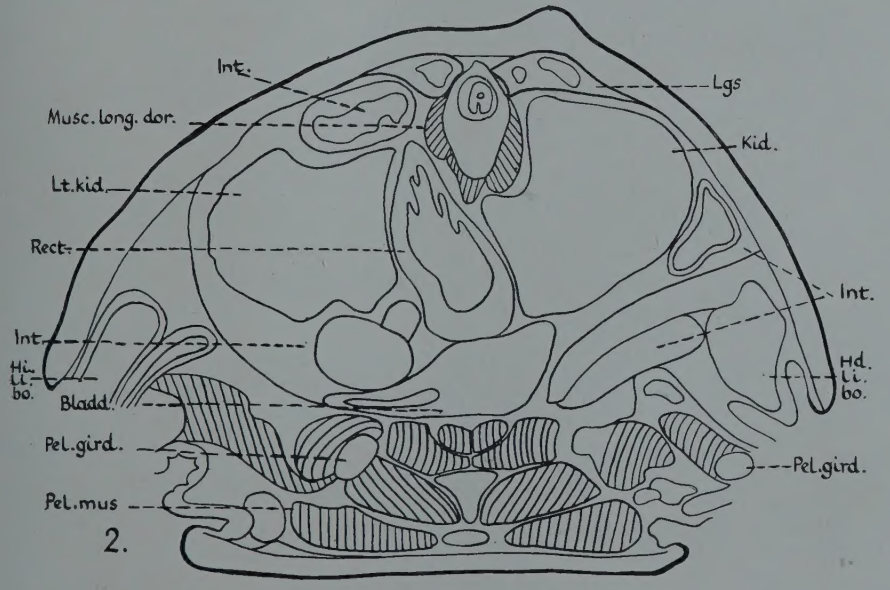
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Pel.gird.
Pel.mus
2.

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